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THE DEMOGRAPHY AND LIFE HISTORY STRATEGIES OF TIMBER ELEPHANTS IN MYANMAR

by

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ABSTRACT

Although the Union of Myanmar is home to the second largest population of Asian elephants (*Elephas maximus*) in the world, the demography of its captive elephant population has never been studied before in any detail. Life history data analyzed in this thesis are taken from the records and reports archived and maintained by Myanma Timber Enterprise, which is under the charge of the Ministry of Forestry, the Government of the Union of Myanmar. The study population contains 5292 individually identified captive timber elephants, which were born or captured between 1952 and 2000. In this thesis, birth origins of timber elephants are referred to as wild-caught and captive-born. Life-table analysis indicates that the captive-born section of the population should be self-sustaining, but that the demographic rates seen in the wild-caught section would not be sufficient to maintain a stable a population. I extend my analysis by conducting detailed survival analyses. Males have a higher mortality than females throughout the age range. In adults, wild-caught elephants suffered significantly higher mortality than captive-born elephants, and their mortality differed by capture methods. Elephants captured by immobilization showed the lowest survival rate when compared with elephants captured by either milarshikar (lasso or noose) or stockade. Regarding the causes of mortality, I document that accidents and agalactia of mothers were the primary causes of death in calves, while malnutrition and accidents were the main causes in adults. Exploring reproductive patterns and maternal investment, I find that elephant mothers do not adapt their offspring sex ratio, and that reproductive fitness is lower in wild-caught females than captive-born females. Lastly, I explore how the process of increasing time in captivity influences survival probabilities and reproductive potential in captive elephants, both within individuals and between generations. I report that capture stress causes measurable reductions in survival and fecundity rates up to 12 years after capture, as well as reducing the survivorship of calves born to captured females. To achieve a self-sustaining population of captive timber elephants in Myanmar without the need for further capture from the wild, I recommended that Myanma Timber Enterprise re-evaluates elephant management strategies, aiming to improving both the fecundity and survival of captive elephants in all age groups.

TABLE OF CONTENTS

List of figures

List of tables

Chapter 1. General introduction

1.1. Introduction

The Union of Myanmar (formerly known as Burma), with an area of 676,553 square kilometers is one of the largest of the mainland Southeast Asian countries, where elephant draught power has been utilized extensively in timber harvesting for more than a centaury (Mar & Win, 1997; Yin, 1972). The single largest remaining population of captive Asian elephants (*Elephas maximus*) is found in the timber camps of Myanmar (Blower, 1985; Toke Gale, 1971; Yin, 1972). Successive Myanmar governments have practiced selective logging system (now known as the Myanmar Selection System) since Burma was one of the colonial states in the early eighteenth century (Bryant, 1996). The harvesting of teak (*Tectona grandis*) from natural forests has been a major source of export earnings for Myanmar for many decades (Eh Dah, 2004)

Elephants play a crucial role in the forestry sector of Myanmar and the benefits from using them are far-reaching (Blower, 1985, Sukumar and Santiapillai, 1993 and Santiapillai and Ramono, 1992). U Toke Gale (1971), a renowned Burmese forester and author of "Burmese Timber Elephants" praised logging elephants as Nature's greatest and the most generous gift to Burma. Some likened the Asian elephant to an amphibious, weatherproof, multipurpose, four-legged machine which is the jungle's perfect cross-country vehicle (Santiapillai, 1992; Sukumar & Santiapillai, 1993). There is a growing recognition of this merit, particularly in the forest industry where the animal can extract timber with much less incidental damage to the environment than rapid but wasteful and costly machines (Mar *et al.*, 1997). Animal skidding (towing logs across the ground by animal) is universally accepted as the most economical and environmentally friendly method of logging, captive elephants will continue to play a vital role in the timber extracting operations in Myanmar for the foreseeable future, particularly in mountainous and swampy areas (Aung & Nyunt, 2002; Mar & Win, 1997).

Although Myanmar is home to the largest population of captive Asian elephants in the world, there has previously been no detailed study of its population demography. Indeed, there have been relatively few attempts to evaluate quantitatively the life histories of any long-lived animals (Cole, 1954), simply because it is rare to obtain long-term datasets on individually marked animals (Gaillard *et al.*, 1998; Mahoney & Schaefer, 2002). This thesis seeks to fill this gap, exploring the demography and life history strategies of captive elephants used in the logging industry of Myanmar.

Life-history data of captive timber elephants, analyzed in this thesis are taken from the elephant log books and annual extraction reports archived and maintained by the Extraction Department, one of the departments of the Myanma Timber Enterprise. The traditional elephant log books given to individual elephant after taming training are equivalent to the 'studbooks' kept in Western zoos. State ownership of thousands of elephants over half a century makes it possible to compile and transfer biodata of all registered individual elephants from the log books to a computer spreadsheet, which later becomes the 'studbook', a database containing a chronology of a captive population, listing vital information on animal identities, sex, parentage, birth and death dates and ages. Additional information on capture methods, place of capture, and annual rate of capture, births and deaths are copied from departmental annual reports.

This database contains the most comprehensive and detailed record of demographic data available for any elephant population in the world, and is effectively the world's largest studbook on Asian elephants. Given the current declines in captive and wild Asian elephants, it is extremely unlikely that the data amassed within this database could ever be replaced or replicated. I am fortunate in having access to the Myanmar elephant studbook, which contains 8006 elephants born and captured between 1942 and 1999. Data recorded for each individual include:

1. Registration number of elephant
2. Name of elephant
3. Origin (wild-caught or captive-born)
4. Date of birth
5. Place of birth
6. Mother's registration number

7. Mother's name

8. Method of capture (if it was a captured elephant)

9. Year of capture

10. Place of capture

11. Year or age of taming

12. Date of death or last known date alive

13. Cause of death.

While the ages of captive-born elephants are known because precise dates of birth are recorded, elephants caught from the wild are aged by comparing their height and body condition at the time of capture with captive elephants of known age, a technique frequently used by other researchers (Wemmer & Krishnamurthy, 1992; Wemmer *et al.*, 2006). Shoulder height is generally believed to equal twice the circumference of one of the fore feet, or the sum of the circumferences of the right and left forefeet (Kurt & Kumarasinghe, 1998), or 2.03 times of the circumference of one of the fore feet (Sukumar *et al.*, 1988).

In wild elephants, shoulder height is considered a valid age criterion (Kurt & Kumarasinghe, 1998; McKay, 1973). For captive-born elephants, body mass and height are thought to be influenced by individual life history and living condition in captivity (Kurt & Kumarasinghe, 1988). Similar to those born in the wild, calves born in captivity are cared for by their biological and allo- mothers and herd mates. These calves enjoy sucking, until the mothers' lactation no longer supports their demands. After the cessation of mothers' lactation, they start foraging and feed for themselves *ad libitum*. It is assumed that the growth rate of those calves born in captivity and those captured from the wild are similar until age 5. For older (>5yr) elephants, the greater foraging opportunities and lack of stress in wild elephants could lead to better body condition and higher body weight than captive-born elephants (Sukumar *et al.*, 1988; Sukumar & Ramesh, 1992), so that elephants which spend their pre-pubertal years in captivity attain a lower maximum height on the average compared to elephants in the wild or those captured after age 10 years. However, age estimation of wild-caught elephants in Myanmar is traditionally done by experienced mahouts, elephant trainers and catchers. According to these experts, height alone is not sufficient to estimate the age of an elephant. The extent of depigmentation (freckles) on trunk, face and temporal areas, and the degree of folding of the upper edge of the ear increase with age, while hairiness of the tail tuft and degree of corrugation or wrinkliness of the skin reduce with increasing age. The Myanmar elephant catchers and trainers take careful consideration of all physical features in estimating age of wild-caught elephants.

It is not possible to use all animals (n=8006) in the original dataset for several reasons. About one-third of the records were excluded from analysis due to missing information on dates of birth, death or capture (n=2711); the majority of these exclusions were wild caught elephants captured before 1950, whose dates of capture are recorded only to the nearest decade. A much smaller number of records were excluded because, although records were complete, impossible values indicated errors in recording. These errors were indicated by dates of death earlier than dates of capture or birth (n=85), dates of parturition earlier than the mother's birth or later than her death (n=150), and by interbirth intervals less than the minimum authenticated gap of 1.5 years (n=8). Where any of the latter two problems arose, the mother and all her births were excluded from analyses of fecundity. While it was possible to exclude these visible errors, it is certain that a small number of transcription errors remain in the data analysed. However, such errors in transcription are as likely to overestimate lifespans and birth rates as to underestimate them, and there is therefore no reason to expect that these errors introduce any bias to the analyses presented in this thesis.

1.2. Background information

1.2.1. The historical and current status of captive elephant populations

Archaeological findings indicate that since earliest recorded times, people have been fascinated by the size, strength and sheer grandeur of the elephant, the largest land mammal. It is said that Asian elephants were brought into captive environments over 4,000 years ago (Carrington, 1959; Csuti, 2006; Lahiri-Choudhury, 1991, 1999; Sukumar, 2003a; Tennent, 1867). According to one hypothesis, elephants were initially pressed into service for "noble" duties: warfare, tiger hunts and the unrivalled prestige of being the mount of chiefs. The earliest evidence of the taming of the Indian elephant goes back to the second millennium B.C (Sukumar, 1989a, 2003a). By the second half of the millennium, large numbers of captive elephants were held by emperors, primarily for use in their armies and it became a tradition for nobles and royals to own elephants (Douglas-Hamilton, 1972, 1989; Kurt, 2006). The emperor Chandragupta, who ruled India from 321-297 BC, is said to have owned 9,000 war elephants. Ralph Fitch, in 1587 probably the first Briton to arrive in Burma, documented that the King of Bago (currently known as Pegu) owned 5,000 war elephants, including three white elephants. The use of war elephants continued in Asia for centuries but their usage as war machines declined with the widespread introduction of firearms in the 1500s. The total number of elephants captured by humans since the 16th century is estimated at between two and four million elephants. In the last century alone, it is estimated that well over 100,000 Asian elephants have been captured for work and zoological exhibitions (Sukumar, 1989a, 2003a).

Intensive exploitation, coupled with enormous habitat destruction, has caused a massive decline in the Asian elephant population in the wild. The magnitude of decline has been far greater for Asian than for African elephants *Loxodonta africana*, which have been subject more to hunting pressure, but have suffered less habitat loss (Sukumar, 1989a). About 0.5 million *Loxodonta* still inhabit a relatively large proportion (22%) of the African continent, with their range of habitat estimated at ≈ 5 million km^2 (African Elephant Status Report, 2002), although their numbers are also declining (Douglas-Hamilton, 1989), whereas >53,000 *Elephas* are now confined to a range of about 0.5 million km^2 in the Asian continent (Sukumar, 2006).

1.2.2. Global population

The Asian elephant, *Elephas maximus* is distributed discontinuously across the Asian continent, in India, Nepal, Bhutan, Bangladesh, Myanmar, Thailand, Peninsular Malaysia, Sabah, Kalimantan, Cambodia, Laos, Vietnam, China and islands of Sumatra (Indonesia) and Sri Lanka. The total wild population is 38,500-52,500, with a further ≈ 16,000 in captivity, the majority of which are in range countries. India has 60% of the global population of wild Asian elephants (Sukumar, 2006).

Myanmar is home to the largest population of captive elephants with an estimated total population of around 5,000. The reported total numbers of captive elephants in Thailand, India, Laos, Cambodia and Indonesia are ≈ 3,500-4000, ≈ 3500, 1100-1350 and >500 respectively, and about 200 each in Indonesia, Sri Lanka, Nepal and Vietnam, according to the country reports submitted at the Elephant Range States Meeting in Malaysia (24-26 January, 2006) organized by the IUCN/SSC Asian Elephant Specialist Group (Sukumar, 2006). These elephants are living in different facilities, such as logging camps, nature reserves, village communities, temples, training centres, zoos, tourist resorts and even individual households (Sukumar, 2003a). There are about 1000 elephants outside the range states of Asia in circuses, zoos and safari parks worldwide (Sukumar, 2006).

1.2.3. Myanmar population

Before World War II the number of working elephants in Myanmar was significantly higher than nowadays (Lair, 1999). Estimates of pre-war numbers can be found in various sources:

i. 2000-3000 elephants owned by a British teak firm, Bombay Burmah Trading Corporation (Evans, 1910)

ii. 1507 elephants owned by one of the British teak firms (Hundley, 1922, 1935)

iii. 6000 adult working elephants in the whole country (Williams, 1950)

iv. ≈10,000 working elephants, 6500 full-grown elephants and 3500 sub-adults (Toke Gale, 1971)

v. ≈7000 elephants (Anon., 1982)

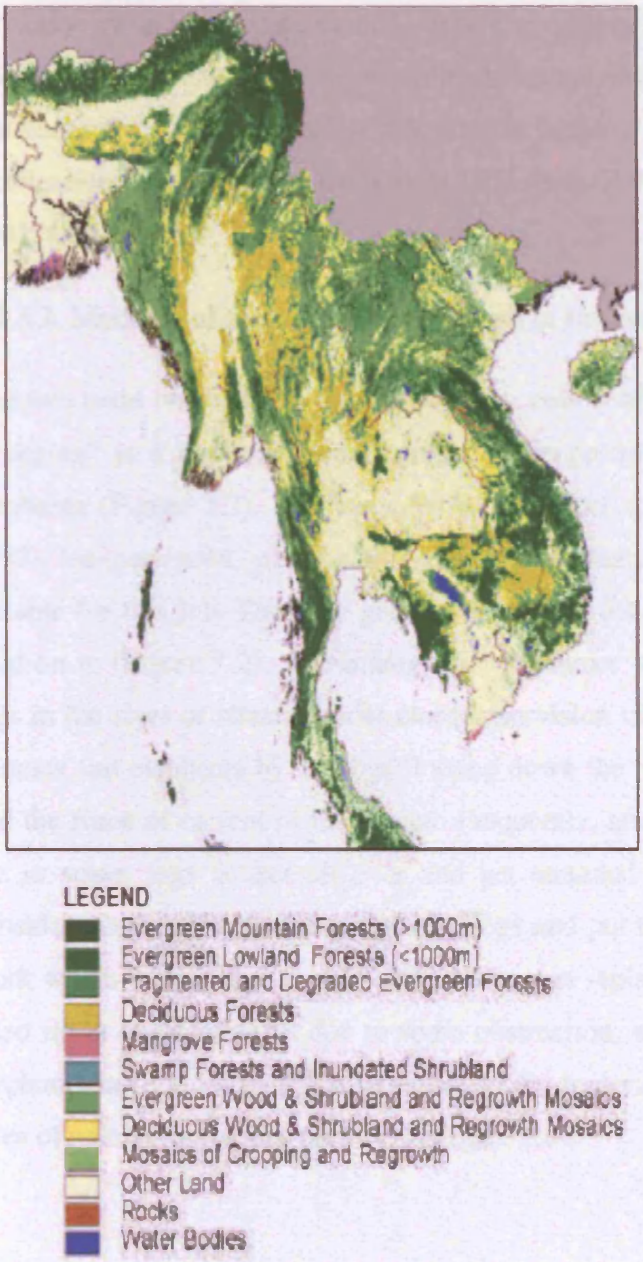
By the end of the war in 1945, only 2500 full-grown elephants, less than half of their pre-war strength, were available for timber extraction work (Toke Gale, 1971). It was said that, during the war from 1943 to 1945, many of the timber elephants died of overwork and under-nourishment, while some died at the hands of Japanese soldiers (who shot them indiscriminately for their tusks) and others were released into the jungles by their owners (Toke Gale, 1971). The most recent estimate of captive elephants in Myanmar shows >5000 (Sukumar 2006).

1.2.3.1. Origin and history

The Union of Myanmar, situated between 9°53' and 28°25'N latitude and 92°10' and 101°10'E longitude, borders with Bangladesh and India in the West and China, Thailand and Laos in the East. It is rimmed by mountain ranges in the north, east and west, forming a giant horseshoe. Enclosed within the mountain barriers are the flat lands of the Ayeyarwaddy, Chindwin and Sittaung River valleys with an extensive network of feeder streams, where most of the country's agricultural land and population are concentrated. Myanmar is one of the most forested countries in mainland South-east Asia and the vast and relatively intact forests of the region are reputed to be among the last strongholds for large mammals such as tigers and elephants (Leimgruber *et al.*, 2003; Leimgruber *et al.*, 2005). Approximately 75 percent of the country lies within the tropics and the remainder lies in the subtropical and temperate zones. The annual rainfall is 900 mm in the dry zone and over 5,000 mm in the coastal region and other parts of the country. The average temperature is below 10°C in the hilly region and over 40°C in the central dry zone in the middle of Myanmar. The great variations in rainfall, temperature, soil and topography result in six major forest types, namely tidal (mangrove), tropical evergreen, mixed deciduous, dry, deciduous dipterocarp and temperate evergreen. Among them, the mixed deciduous forests are economically the most important, being home to high-value species such as teak (*Tectona grandis*), rose wood or pyinkado (*Xylia dolabriformis*) and iron wood or paduak (*Pterocarpus macrocarpus*) (Figure 1.1).

Elephants were given protection in Burma (Myanmar) under the Elephant Preservation Act (1879) and Amended Act of 1883, which was prescribed by pre-colonial governments. There was no far-sighted conservation strategy in those days. Preservation of wild elephants was carried out simply for the sake of maintaining a viable population of wild elephants to replenish the stock of timber elephants as and when necessary. The idea of elephant hunting as a sport of the upper classes, alien to the local ethos, was introduced by the British during the early nineteenth century (Sukumar, 2003a). Big-game hunting was a cultural phenomenon among colonial rulers across the Indian subcontinent, Burma and Sri Lanka at that time. The Elephant Protection Act was later superceded by the Burma Game Rule (1917). As a result, sports licenses were freely issued and many elephants were lawfully and unlawfully killed (Zaw, 1997).

Figure 1.1. Forest cover map of Myanmar (Stibig & Beuchle, 2003)



After Burma gained independence, successive Burmese Governments have granted added protection to both wild and captive elephants under the Elephant Registration Act (1951), Burma Wildlife Protection Act (1936 and Amended Act of 1956), Forest Law (1992) and Protection of Wildlife and Wild Plants and Conservation of Natural Areas Law (1994), declaring that elephants are completely protected animals, prohibiting hunting, except by license to capture only for scientific or research purposes. The issuance of a game license is totally banned. Registration of privately owned and state-owned captive elephants is conducted under the authority of the Ministry of Forestry. With regard to international obligations, Myanmar has been a party to the Convention of International Trade in Endangered Species (CITES) since 1997 and the Convention on Biological Diversity (CBD) since 1994 (Aung & Nyunt, 2002; Aung & Nyunt, 2001; Ugga, 2000).

1.2.3.2. Methods of utilization of elephants in timber industry

The two main tasks for elephants during the course of extraction are "*aunging*" and "*yelaiking*". "*Aunging*" is a Myanmar word, referring the pushing of measured logs by the foreheads of elephants (Figure 1.2). It is regarded as the most strenuous of all timber operations (Ferrier, 1947). Inexperienced, young adults, pregnant elephants and females with sucking calves are not suitable for this job. The only gear necessary for actual *aunging* is a girth rope for the rider to hold on to (Figure 1.2). "*Yelaiking*" is a Myanmar word for an operation to clear the jammed logs in the river or stream, under close supervision of ground staff, in order to avoid injuries to humans and elephants by the logs floating down the river. Free floating of logs depends on rain and the force of current of the stream. Frequently, after heavy downpours and when the streams are in spate, logs scatter all over and get stranded on sand or mud banks. When the spate subsides, elephants collect the scattered logs and put them back into streams. This is the kind of work which no machine can do and nothing can replace the elephants here. Sometimes logs are piled up in huge log-jams due to some obstruction, such as boulders in the stream. Here again elephants have to be called in to break up the log-jams, which involves tremendous risk to the lives of animals as well as the riders (Figure 1.3).

Figure 1.2. "*Aunging*" or the pushing of logs by the foreheads of elephants

Figure 1.3. Elephants clearing log jams in streams

All the extracted logs cannot be floated down in one rainy season. At the end of rainy season, around November and December, elephants are employed again to drag logs which are left behind and scattered in and along the river to nearby river banks and place them in an orderly way, to be ready for floating in the next rainy season.

Timber elephants are used in two of the four different stages of timber extraction. **The first stage**

of timber extraction involves felling of girdled and seasoned trees. Felling is done in the rainy season by hired local timber-jacks, who own simple felling equipment such as cross-cut saws and axes. The felled logs are taken away from the stump of the felled tree up to wider paths which can be used as transit. This work is termed "stumping", mostly done by elephant draft power, and **is the second stage of extraction (Figure 1.4)**. Normally stumping is done by first class elephants or elephants at their prime age (see Table 1 for details of elephant class definitions).

Figure 1.4. Stumping, as the second stage of extraction

From the transit paths, logs are dragged by second or third class elephants (see Table 1.1) to the measuring points, where logs are measured for royalty payment and settlement of dragging charges for elephants leased from private owners (Figure 1.5). **The third stage of extraction** is transportation of logs from the measuring point to the rafting depots, railway sidings and transit log-yards; elephants are again indispensable in this task.

The **fourth and final stage** of extraction pertains to transportation of logs from main river depots, railway sidings and log-yards by means of rafting, railing and trucking (Figure 1.6) (Zaw, 1997). Buffalo draft power is also used on flat terrain for short hauling distances and smaller logs (Evans, 1910; Toke Gale, 1971; Zaw, 1997). Hard woods are generally transported by trucks or by flatbed trains. Teak is floatable when dried or seasoned, so that they are transported or by rafting.

Figure 1.5. Logs at a measuring point

Figure 1.6. Transport of logs by rafting and trucking

The working elephants are generally classified by two methods; (i) according to age or (ii) according to their working (hauling) capacity. Calves under 4 years are known as calves-at-heel (CAH). Sub-adult elephants under 18 are classified as trained-calf (TC), which are sub-divided into light transport animal (5-14), and baggage-cum-light extraction apprentice elephant (15-17). Trained calves (age between 5 and 17 year) are mostly used in transporting the personal equipment of the staff involved in timber operations and rations for the elephants in the rainy reason and early winter season before the construction of logging roads. The hauling capacity of a prime aged adult elephants is many times higher than their carrying/loading capacity. They can easily haul logs weighing nearly their body weight but they cannot carry a load weighing half a ton (Evans, 1894). According to Kerala Captive Elephant Rules (2003), maximum load, inclusive of gears/saddle and riders for an adult elephant (>2.25 m at shoulder height) is set at 400 kg (source: http://www.keralaforest.org/html/actsandrules/kce.pdf). According to Ferrier (1947) and Evans (1894), the maximum loading capacity depends on the nature of the terrain, time of the day, time of year, existence of shade, water, fodder en route, and presence or absence of fatigue from previous journeys. For elephants, aged between 5 and 12 years, loading should not exceed 30 kg and they are not encouraged to travel in rough terrain. For elephants, aged between 12 and 15, loading capacities are respectively 70 kg, 45kg and 30 kg in plain areas, hilly regions and steeper terrain. For those aged 16 and 17, a maximum loading is set at 100 kg. For all age groups, distance of traveled per day is set by terrain type, with a maximum of 25 km/day for flat plains, 16 km/day on steep or muddy paths, and not more than 3 strenous marches without a rest period. (Source: Standing orders, Myanma Timber Enterprise). Ferrier (1947) stated that the mahout should unload promptly and massage the spine for a few minutes at the end of each journey while the elephant cools down.

Full grown elephants over 18 are again sub-divided according to age, intelligence and hauling power. In general, a full grown elephant drags 100 to 180 hoppus tons per animal per year for teak logs, or 180 to 240 hoppus tons per animal per year for other hard woods. Elephants aged 18-24 are good for light extraction work, 25-30 year olds can be employed on hilly terrain, those aged between 30 and 45 are regarded as prime-aged (first-class) which are able to drag a log > $3.5m^3$, while those aged between 46 and 53 are regarded as post-prime age as their dragging efficiency is declining rapidly with age. Those aged between 53 and 60 are not fit for heavy work and are given mild duties. Working elephants are given retirement at age 60 (Aung & Nyunt, 2002; Ferrier, 1947; Toke Gale, 1971)

The other classification of timber elephants is based on their working or hauling capacity. Hauling capacity is calculated by the volume of timber (Ferrier, 1947; Toke Gale, 1971) or by hoppus ton (Aung & Nyunt, 2002) (Table 1.1).

Table 1.1. Classifications of elephant based on age and dragging capacity (1 hoppus ton = 1.8 m^3).

Class	Age range	Dragging capacity
First class	30-45	> $3.5m^3$
Second class	25-30, 46-53, weaker elephants aged 30-45	2-$3.5m^3$
Third class	18-24, weaker elephants aged 46-53	< 2 m^3
Fourth class	>53 Poor and disabled elephants of any age	None – light baggage carrying only
Fifth class	Trained elephants 5-17	None – light baggage carrying only
Sixth class	Calf-at-heel <4	No work load

Working months for elephants are from 15th June to 20th February with a rest of three weeks at the end of October, depending upon the temperature and locality. Ferrier (1947) stated that during the pre-independence era, Burmese timber elephants worked a maximum of 160 days per year. The usual pattern of working days is 5 days work and 2 days rest in a week. When the elephants return from summer rest camps they are worked for 4 hours a day in the first week, then 6 hr per day in the second week, and in the third week and thereafter, they should be assigned to full duty but not exceeding 8 hr per day in cool weather and 5 hr per day in hot weather. The amount of work an elephant can do in a day depends on its general health and strength, the size of timber, the state of the drag path, the nature of the terrain, quality and quantity of fodder available in the vicinity and the season of the year. No elephant is allowed to work beyond 10 am in the morning session and earlier than 3 pm in the afternoon sessions during hot-weather months. In all timber extraction operations, everything must be done to help the animal by well-made dragging paths, intelligent use of rollers, block and tackle for uphill drags and the use of two or more elephants in tandem to drag large logs (Toke Gale, 1971).

1.2.3.3. Capture methods

According to Sukumar (2003) and Lahiri-Choudhury (1999), the earliest evidence of the human-elephant relationship is from around 1500 BC, when Indo-Europeans, a pastoral people from Central Asia, reached the Indian Sub-continent. The story can be traced in the hymns, prayers, poems, rituals and in the series of compositions known as "*Vedas*". As the ownership of an elephant was a status symbol, the capture of the elephants was an acceptable practice. Capturing elephants with the help of trained elephants (*koonkies*) is known from that time.

In Myanmar, the capture of wild elephants is strictly controlled by the Forest Department through the Elephant Control Scheme, a system dedicated to the protection of crops and public property by controlling the wild elephant population within the carrying capacity of the forest they inhabit (Olivier, 1978; Zaw, 1997). In the early 1960s, capture operations were carried out by private capture teams, except immobilizations, which were run by the staff of the Timber Corporation (Anon., 1982). The animals caught by these private teams were sold to the Timber Corporation. The average rates at that time were: kyat 3000 (equivalent to US$ 600) for an elephant under 1.37 m height at the shoulder, kyat 7,000 (US$ 1,400) for those between 1.37 m and 1.68 m, and a further kyat 2,400 (US$ 450) for each additional 0.30 m above this (Anon., 1982). The number of captures was limited to 200 elephants per year for 1974, 75 per year for 1980/81, 150 per year for 1981/82, and 120 per year for 1982/83 to 1989/90. Information is not readily available on the current value of live elephants in Myanmar.

Capturing wild elephants is usually practiced in the cool season (October to January) and never during the monsoon and summer, due to practical difficulties (Toke Gale, 1971). There are five methods of capturing wild elephants in the range states of Southeast Asia, namely stockade, milarshikar, immobilization, decoy and pit method. Decoy and pit methods (Figure 1.7) were used occasionally soon after World War II in southern Myanmar, Cambodia and Sri Lanka (Toke Gale, 1971), however only the first three methods have been commonly practiced in Myanmar, and these are described in detail below.

Figure 1.7. Capture by pit method (a) Large pits are dug in/near elephant pathways. Bottoms are lined with several feet of leafy branches to cushion the fall (b). Branches are again added to the pit to create a walkway out and with the assistance of a koonkie elephant pulling, the captured elephant is led out of the pit

1.2.3.3.1. Stockade method

The stockade method, known as *kheddah* in Hindi, and *kyone* in Myanmar, was the predominant capture method traditionally used by private elephant catchers of the Karen ethnic minorities (living in the middle and southern parts of Myanmar) until 1985, when the Myanmar

Government officially stopped using this method due to the high number of fatalities reported during the capture operations (Aung, 1997). In old literature, the stockade is termed corral (Tennent, 1861, 1867). The stockade method is a cost-effective way of capturing wild elephants by driving the whole family unit into a stockade. A stockade team consists of about 30 men. No helper/trained elephants (*koonkies*) are used in this method. An ideal site for the construction of a stockade is flat terrain with an abundance of shade, fodder and water; it should have easy access for baggage elephants, allowing rations, medicine and construction equipment to be carried in without difficulty. According to Toke Gale (1971) and Tennent (1861), the whole contraption is roughly shaped like a huge capital Y, with two very long arms or railings (350-550 m) forming a wide funnel, also known as *wing of Kheddah*, and the short leg of the Y creating a narrow holding area or enclosure. The short leg is about 3.5 m wide at the mouth and gradually tapers off to a dead end where the width is less than 2 m. Such a stockade can hold up to 15 individuals (Figure 1.8,a and 1.,a).

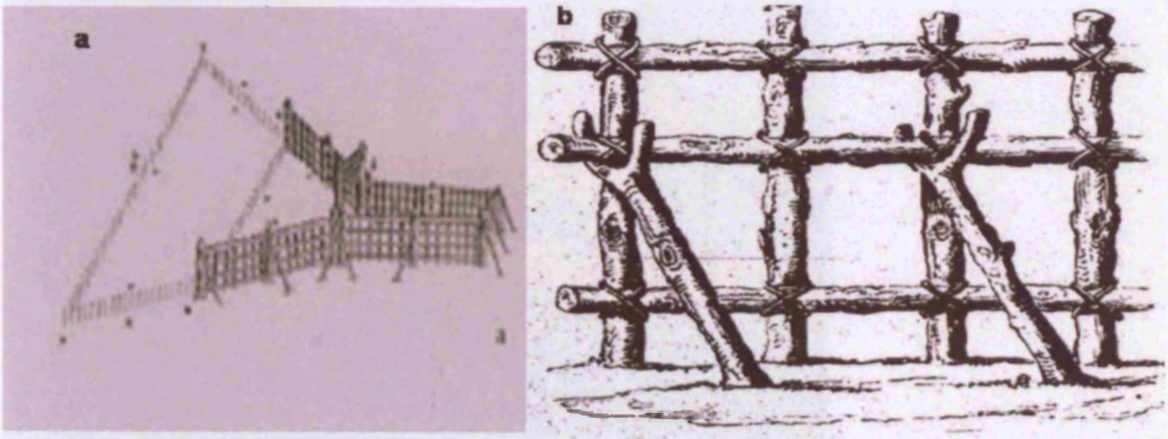
The stockade is made of standing trees or posts 4 to 5 m in length and 0.30 m or more in diameter. These posts are dug three or four feet into the ground and spaced at intervals of a foot or so (Figure 1.8,b). They are then reinforced with a set of poles of similar size, and fastened together horizontally with strong strands of cane and jute (*shaw*) ropes (Figure 1.8,c). Like the vertical posts, the horizontal ones are also placed at intervals of one to two feet, starting from the ground right up to the top, and forming a powerful lattice work of saplings (Figure 1.8,c and 1.9,a). On one side of the holding area of the stockade, an opening large enough for an elephant to go through is created with a door that can be easily shut or opened (Figure 1.10). Traditional elephant catchers construct the whole stockade without a single nail. All materials (post, cane, shaw) come from the jungle.

At the point where the long arms join, there is a heavy drop-gate closing the entrance (Figure 1.9, b). It is made of large straight tree stems and suspended some 9 m above the ground by means of a 15 cm thick coir-rope. This rope, which is 25 m in total length, is thrown over the beam that spans the entrance and then stretched taut over the entire length of the stockade and fastened round the stout tree that supports the narrow end. When this rope is severed, the drop-gate forcefully and swiftly closes the holding area. A small platform or bridge about 1 m^2 is built precariously on top of the entrance where the gate-keeper, usually the team leader, is stationed at the time of drive. He needs to cut the rope with a sure stroke using very sharp knife.

The selected herd is gradually coaxed towards the stockade by shouting and by blowing horns made of bamboo. Once the herd enters into the funnel of stockade, the drive is intensified with much shouting and beating of empty bins. The main object is to keep the herd in front of the beaters all the time. To direct the elephant herd straight into the stockade and to prevent them turning back, members of stockade team set on fire dried twigs, leaves and branches which have been collected before the drive. The huge flames cause the frenzied animals to rush blindly forward with never a thought of turning back. When a group of elephants has rushed into the stockade and there is no animal directly under the drop-gate, the gate-keeper, stationed on top of the entrance cuts the coir rope to force the drop-gate to fall on to the ground.

In general, the stockade team tries to take out the elephants as soon as possible, which is normally within 24 hours, because undue delay could cause additional injuries and stress to captured animals. One animal at a time is forced out of the opening made in the side of the stockade and removed to nearby "cradles" designed for breaking procedures (Figure, 1.11 and 1.17).

Figure 1.8. (a) Schematic diagram of a stockade (Kurt, 2005) and (b) detail of stockade construction (Tennent, 1867); the fences are elephant-proof constructions made without using nails, but fastened together horizontally with strong strands of cane and jute ropes (c).



(c)

Figure 1.9. General structure of a stockade (a), with drop-gate heavily camouflaged by leafy branches along the fencing of the driveway (b and c)

(a)

Due to the nature of the operation, the mean capture age by the stockade method is higher than that of the other two methods. Most elephants captured by stockades are females, including matriarchs, pregnant females, juveniles and mothers with suckling calves (Figure 1.12). Most private elephant catchers avoid males with tusks, because adult males, when blind with fury and fear, are liable to injure or kill other elephants in the stockade, and are also harder to tame.

Kheddah capture was reported as the most destructive of the three capture methods (Lair, 1999) because of high mortality rate during the capturing process (Aung, 1994). Among 1,042 *kheddah* captures conducted between 1970 and 1992, the mortality rate was reported as 30.1% (Aung, 1997; Lair, 1999), while other put the rate at 60% (Blower, 1985), blaming lax supervision by government officials during and immediately after capture operations (Lair, 1999).

Figure 1.10. One elephant is taken out at a time from the holding area of stockade using man power.

Figure 1.11. Breaking follows capture

Figure 1.12. Females with suckling calves are sometimes captured by the stockade method

1.2.3.3.1. Immobilization method

Historically, Etorphine hydrochloride has been the drug of choice for immobilizing free-ranging elephants (Fowler, 2006b; Fowler *et al.*, 2000; Kock *et al.*, 1993a; Page *et al.*, 1994; Schmidt, 2003). Etorphine is a highly potent opiate-derived narcotic analgesic, producing pharmacologic effects similar to those of morphine, namely, depression of the respiratory and cough centres, decreased gastrointestinal motility, elevated blood pressure, tachycardia, and behavioural changes. Its use was first reported in 1961 (Harthoorn *et al.*, 1961). The drug and the CapChur projector capture-gun were introduced to Burma by Dr. Harthoorn in 1968, then the world's most renowned expert on capturing big-game animals (Toke Gale, 1971), when the first batch of 24 elephants were captured. The recommended dosage is 1 mg/450 kg (0.0022 mg/kg) for a well-trained tamed Asian elephant (Kock *et al.*, 1993a; Kock *et al.*, 1993b). In field situations, higher doses are advised (approximately 1 mg/400 kg) rather than risk under-dosing and losing contact with the elephant. Under-dosing in a free-ranging situation is particularly hazardous. The under-sedated wild elephant is at high risk of suffering the effects of sedation in hazardous terrain, such as a narrow ravine or gorge, which can cause a slow death, if fall into.

'Time to sternal recumbency' is the interval between administration of the drug and the point at which the depth of immobilization is sufficient to cause recumbency in the animal. When capturing elephants, the capture team prefers a time to sternal recumbency of not more than 20 minutes in order to reduce the flight distance. Calculating the correct dose for a wild elephant can only be a guess, based on prior experience or by comparing the body mass to the known body weight of a captive elephant. Under-dosing may result from several causes, including underestimating the weight of the elephant, failure to inject the full dose, needle breakage without full injection, or depositing the drug in poorly vascularized tissue (fascia, fat). It gives the elephant more time to feel the effects of the drugs, giving it a further flight distance. When the sedated elephant is found, the capture team tethers it in the shortest possible time (Figure 1.13). The whole tethering procedure must not last more than 30 minutes in order to keep the sedation effect to the minimal possible time. A reversal drug (diprenorphine 2-4 times the dose of etorphine) is given intramuscularly. The team has to wait until the wild elephant can stand steadily on its legs. With the help of trained elephants (koonkies), the captured elephant is dragged to the nearest base camp.

Figure 1.13. Capture by immobilization

1.2.3.3.2. Milarshikar (lasso) method

This is the traditional elephant capturing method of Assam, India and the northern part of Myanmar. In the Assamese language, "milarshikar" refers to hunting in an open field situation without erecting a stockade (Tennent, 1861). In Myanmar, it is known as *Kyaw hpan* method.

Essentially the method involves chasing wild elephants using trained elephants (koonkies) and noosing them when the opportunity arises (Figure 1.13). Only 13% of the total elephants in this study population are captured by the milarshikar method, which was only practiced in the remote areas of northern Myanmar. The capture team is composed of six men with three highly trained koonkies, a tusker and two females or tuskless males. When the wild herd is sighted, the team atop koonkies identify which elephant should be captured. Then the team chases the elephant herd. The objective is to wear out the elephants or to force them towards a hilly region or a big river or any other area where their movements are restricted. A target elephant (usually in the height range of 1.7 to 2.3 m) is selected and attempts are made to isolate it from the herd. Once the target elephant is isolated, the *phandi* (noose handler) throws a *phand* (noose) over the neck of the elephant and tries to restrain it with the help of the koonkie. During the entire operation, the phandi occupies the front seat on the elephant and the mahout controls the koonkie from its back. He also keeps watch over the other wild elephants while the phandi is busy with his quarry. It is then dragged to the training depot with the help of one or two koonkies. The captured elephant is treated for injuries, if any. The wild elephant remains at the depot for 3-4 weeks during which period it is familiarised with human touch and voice through different rituals involving caressing and the recital of folk songs.

Milarshikar is not suitable for capturing mature adult elephants above 2.3 m shoulder height because they are likely to suffer higher stress and trauma than young elephants (<2.3m in height) during capture and breaking procedures. Tuskers, suckling calves, pregnant cow elephants and mothers with suckling infants are not chosen. Milarshikar involves considerable risk for personnel involved and cases of injury and even death are not uncommon. There is also a chance of the captured wild elephant becoming suffocated if the knot of the noose is not correctly placed.

In terms of the methods of capture used, both milarshikar and stockade were officially banned in 1985 and immobilization became the sole method of capture. After the introduction of the immobilization method in 1968, Myanmar Timber Enterprise set the minimum shoulder height for captured elephants at 1.37 m, with the estimated age of around 5 year. There was less restriction on age and size of wild-caught elephants in the early 1960s and elephants older than 40 could be caught by money-minded private capture teams.

Figure 1.13. Capture by milarshikar method in Myanmar

1.2.3.4. Taming methods

All captured elephants undergo a taming procedure immediately after capture. Tameness is defined as "having no flight/fight tendency with respect to man" (Hediger, 1964). Older wild-caught elephants may be more difficult or take more time to tame than those born in captivity because of prior negative experience with humans. The taming or breaking procedure, therefore, undoubtedly incorporates stress and compromises the welfare of the animal, especially during the first few days of taming. Freshly caught elephants and those 4 to 5 year old calves born in captivity are first put into crushes. The trainers use food and water wisely as a reward during the breaking operation. Until thoroughly obedient, which usually takes place after about 3 days, the calf does not see any other elephants. Later on, trained elephants are brought alongside the crush and fed and handled in full view of the captive. As soon as it has learned to be obedient, the trainee is taken out of the crush, but held loosely through the breast band (cradle) or tied to a tree. Thereafter its progress is rapid. Breaking procedures are normally conducted at night, to avoid heat stroke and unnecessary loss of energy.

The term "breaking" is used for the initial phase of training freshly-caught wild elephants or untrained and misbehaving elephants, to achieve the elephant's total submission to the will of humans. The mahout or handler takes the role of the head of herd, as an alpha animal. It is normal for the elephant to resist training and reject food and water for the first few days. At the end of this period, its spirit is more or less broken and it starts to accept food and water given by the attendants. Male elephants are said to take longer than females to reach this point and are more likely to be traumatized by physical punishment and/or self-inflicted wounds through struggling.

Once the newly-caught elephant accepts its subordinate position, "taming" (the preferred term for the flexible phase of the training procedures) follows. This part of the process is aimed mainly at training the elephant to respond to simple verbal commands, such as "stop", "come", "stand still", "sit", "lie down" etc. Freshly captured elephants are likely to go through highly stressful and unpleasant experiences for a minimum period of one month, followed by a less stressful learning phase for about 10 years before they are accustomed to captivity and recognize the hierarchal structure and their position as subordinates. It may be assumed that the psychological and physical trauma caused by capture, taming and adaptation to captivity are costly for wild-caught elephants. On the other hand, those elephants born in captivity have a comfortable life-style as they grow up, in a semi-extensive system, and undoubtedly receive enough support from both the members of their maternal herd and from mahouts and possibly their family members. Most captive-born elephants are known to be tractable and easy to train. They rarely undergo harsh breaking procedures, unless they misbehave and are difficult to handle, or attempt to attack humans and other elephants.

Those born in captivity have close contact with humans at an early age, especially if it is in lieu of care-giving via hand rearing or imprinting, as the young learn to copy the mother's positive responsiveness to humans (mahouts) and taming is relative easy and without any rough procedures. Taming is a necessity in elephant husbandry not only to facilitate maintenance and heath care, but also to utilize the animals as draft animals, subordinate to humans. The unpleasant suffering experienced by the wild caught elephants during the breaking procedure is gradually remedied by continued training with positive reinforcement and close contact with mahouts for another ten or more years. During this period, these elephants are used as baggage elephants. . Taming/breaking procedures are best carried out in the cold months of the year (November and December) to avoid heat stress and because of the availability of good quality fodder.

The officer responsible for training and taming must make all necessary arrangements, the most important of which is the selection of a rider (Ferrier, 1947). Heavy riders should not be allotted to small calves (Ferrier, 1947). Essentials for a training site are good shade, plentiful fodder and water and a level area at least 200 m long. Three methods are used in the taming of elephant in Myanmar (1) one-sided or half crush (2) two-sided crush and (3) cradle (sling) method. Normally, crushes are used for captives of 2.1 m and above in height and cradles for those below 2.1 m.

If a one-sided crush (Figure 1.14) is used, trainee elephants suffer less injury but the trainers are at greater risk. *Koonkie* elephants are useful in this operation as they help to restrain the trainee by pushing it alongside the crush (Figure 1.15). In a two-sided crush (Figure 1.16), the risk of trainers being injured by the elephant is lower, but the elephant can be subjected to bruises and concussion as the result of struggling and aggression during the first few days. Two-sided crushes are normally used for aggressive and intractable elephants. They are also useful for general veterinary inspection of tamed elephants.

Figure 1.14. One sided crush

Figure 1.15. ***Koonkie*** **elephants help the trainers to tie up the calf at the crush**

Figure 1.16. Elephant in a two-sided crutch (mostly used for veterinary inspection rather than taming)

The cradle method (Figure 1.17) is the mildest, and is mostly used for calves born in captivity and less aggressive females (Toke Gale, 1971). The "cradle" is a sling made with a breast band of about 0.20 m width, which is one of the components of the dragging gear. It is made from plaited manila ropes or strands of the shaw tree (*Sterculia villosa*). Before being used, the sling or breast band has to be softened with lard to avoid bruising when the elephant struggles during the process (if the crush method is used, all posts are smeared with lard for the same reason).

Three strong posts (0.33 m in diameter and 3.3 m long) with forked ends are set upright in a triangular arrangement 3-5 m apart. A cross bar (0.25-0.30 m in diameter, 4 m long) is placed on top between the forked ends of two of the upright posts and fastened by shaw ropes or cane/rattan strips. Finally, two longitudinal bars (0.33m in diameter, 4-5 m long) are placed 1m apart supported by the cross bar and the third upright post, secured in position with strong ropes.

The calf to be trained is noosed at its neck. The neck noose should be well adjusted to fit the neck, not too loose so that it can slip off, but not so tight as to risk strangulation. With the assistance of koonkie elephants, the trainee calf with neck noose is guided into the cradle. Members of the taming group must fix the well-lubricated sling around the calf's chest while other members tie the ropes at each side of the neck noose and secure these to the upright posts of the cradle, enabling the calf to be stabilized in the middle of the cradle. Body temperature, pulse and heart rate, and the nature of defecation and urination are recorded daily. Nutritious diet and clean water *ad libitum* are provided during the taming training. However, it is normal for a calf to resist taming and refuse to eat in the first few days of the breaking-in process. Any injuries are treated to prevent infection. All taming procedures are usually started in late evening under the light of a camp fire. This practice has been criticized as sleep-deprivation, and thus a cruel and brutal torture. However, the purpose of training by night is not to prevent sleep, but to reduce heat stress, accustom the elephant to fire, which is often used to drive wild animals, and more importantly, to carry out the process at a quiet time with few other people around, thus allowing the elephant to selectively pick up the voices and commands of the men that will become their masters for the rest of their lives. During the first few days, the group of trainers talk softly to the elephants or sing songs, known as *shaw pike* in Myanmar, while rubbing the rump, thighs, belly, chest, shoulders and all parts of body so as to make it familiar to the touching and voices of humans. The mahouts then start to sit, stand or ride on its back or neck (Figure 1.17). After 2 or 3 days of training, the elephant begins to struggle less, and to take food from the trainers, and starts to become receptive to touching. Ropes are still tied to the hind limbs, allowing the elephant to learn the sensation of a tethering chain.

After the first signs of accepting human touch, the sequence of taming training is as follows:

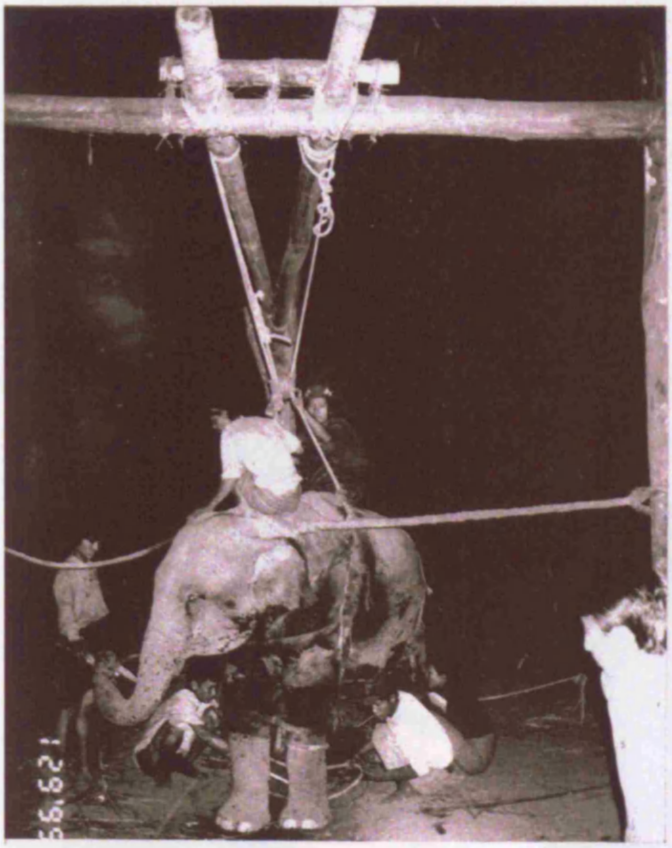
i. Fewer ropes in the hind limbs, the cradle (breast band) is removed and the calf is allowed to learn to stroll with its fetter.

ii. The calf is then frequently transferred to various locations around the training camp, to make it familiar with its environment.

iii. When the elephant becomes more docile and tractable, it is taken to lush pasture and allowed to graze by day, and brought back to camp at nights. During this stage the elephant is closely observed by the trainers to monitor sleeping patterns and its ability to get up and walk comfortably with fetters attached to the front limbs. In the initial stage, the trainee elephant faces difficulties when rising from a reclining position with fetters.

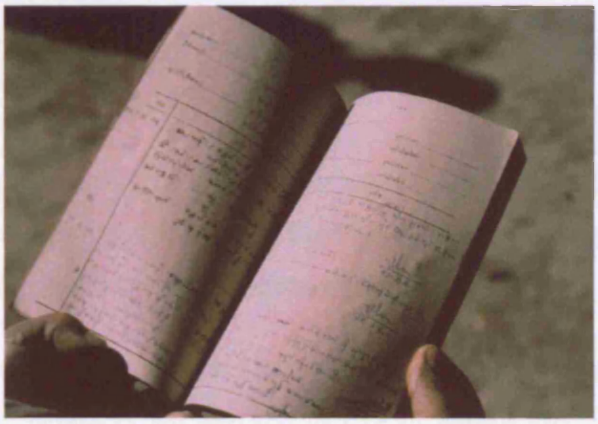
iv. Once the elephant is accustomed to the fettering chain while sleeping, walking and rising, it is allowed to wander freely both day and night. Intensive training is continued to teach simple commands such as lift the leg, lower the front portion (kneel down position), stop, be careful, back up etc., which are indispensable for use as a working elephant.

Figure 1.17. Cradle method to train elephants



After the completion of taming, each elephant is classified as the trained calf (TC) and assigned a permanent individual registration number (which is later branded on their rump as a permanent marker), a mahout and a log book, known as "FORM J" (Figure 1.20,b), in which its biodata (sex, temperament, musth, mating, calving, veterinary intervention etc) are recorded. All government-owned elephants have two branding marks on each rump, star on top and the registration number (Figure 1.18,a). Branding is made by using a corrosive paste, containing light kaolin, bentonite and caustic soda mixed with glycerin and methyl alcohol. It is usually done during the rest period in summer so that the working season is not disrupted. Evans (1910) and Ferrier (1947) gave similar descriptions of chemical branding which includes washing and cleaning of the skin, tying the elephant's tail under its belly, applying the paste and then leaving the elephant in the sun to hasten drying of the paste. The swollen black mark appears within 24 hours and in due course the skin peels off leaving a permanent scar of the branded markings after routine application of dressing oil containing fly repellent and antibiotics. Branding marks help to identify and distinguish tamed elephants from wild counterparts or from private-owned elephants, which normally have their own branding marks.

Figure 1.18. Timber elephant with registration number and a star, branded on its rump (a) and (b) a log book. A star above the numbers denotes Government-owned property



After age 15, they can join the full-fledged working elephant group as apprentices. During the first year, they are taking to a logging site for two days a week with full dragging gear. They are not asked to join the work force but let it observe how other full grown elephants are working. This is the year, the young adults are teaching to get use of wearing dragging gear and the dragging commands used at work site. When they enter age 16, at the second year of apprentice, they are taking to the work site 3 working days a week and are taught how to perform *aunging* and *yelaiking*. When entering age 17, at their third and the last apprentice year, they are trained to drag a log not more than 1.5 m^3 and work 4 days a week. From about 18 to 55 years, a timber elephant is kept in harness five days a week, rain or shine, about a total of 160 days/year with the break of some two months for a spell of rest in hot season and a short break around October/November.

1.3. Elephant keeping systems

1.3.1. The traditional keeping system of captive Asian elephants in Southeast Asia

Traditional systems of elephant management and husbandry vary widely across Asian countries and regions. The main characteristic of the traditional keeping system for captive elephants in Asia is close contact between man and elephant, which is analogous to the Free Contact keeping system of the modern zoo, in which man and elephants share the same work space without any barrier between them (Kurt *et al.*, in press; Schmid, 1998a). The basic principal behind traditional elephant training is that the animal is controlled by a handler through domination (Fernando, 1898; Koehl, 2000). The mahout or handler intentionally takes the role of an alpha animal within the herd.

Depending on the accessibility of foraging areas and the duration of unsupervised and unrestricted free-range mobility, the elephant keeping systems for captive Asian elephants can be defined as "extensive", "intensive" and "alternative" keeping systems (Kurt, 2006).

In **extensive keeping systems**, captive elephants generally live in forest camps. They are used as riding, transport and draft animals. Female elephants are allowed to live in family groups, but sub-adult and adult males are kept singly for a certain period of time during musth. Elephants enjoy unsupervised and unrestricted free foraging at nights, with hobbled front feet, in the nearby forest, where they find food and encounter tame and wild conspecifics. In some parts of South India and in the logging camps of Myanmar, additional fodder is given depending on seasonal availability and quality of forage. Many mahouts belong to tribal societies with a broad knowledge of elephants and their habitats. Accidents rarely happen (Kurt, 1995).

Intensive keeping systems are those in which animals are kept by temples or private owners more or less individually, fed exclusively on prepared fodder, and at night or if idle, shackled with long or short chains by a hind foot or by both one hind and one front foot of opposite sides (Kurt & Mar, 2003; Kurt *et al.*, in press). Retarded growth, signs of stress from hunger, physical, psychological and thermal discomfort, chronic wounds resulting from abuse and misuse of the hook (ankus) are often easily visible. Malnutrition resulting from inadequate and inferior quality of fodder delays puberty and causes infertility in females (Kurt, 2006). Contact with captive and wild conspecifics is unlikely because intensive keeping is concentrated in urban regions and in temples. Restricted movements and the practical absence of contact with conspecifics lead to extreme aggression towards handlers. The mahouts in charge of intensively kept elephants are often underpaid, their knowledge is decreasing fast and many of them are addicted to alcohol and other drugs (Kurt & Mar, 2003). The vast majority of private owners lack knowledge, financial resources and space, and have little interest in keeping the animals humanely (Ghosh, 2005). In India and Sri Lanka, intensively kept elephants are increasingly used in religious processions, political and public demonstrations or wedding ceremonies and used as riding animals for urban tourism. In order to participate at these ceremonies, elephants are walked for several miles or are transported by trucks. Sometimes accidents happen on the way (Figure 1.19). Sometimes, they perform circus tricks or play football. In Thailand, elephant shows mimic war elephants and the noosing of wild elephants by the milarshikar method. The intensive keeping system has been taken over by western circuses and in former times also by zoological gardens.

Figure 1.19. In South India, only bulls are traditionally participated in ceremonies. Accidents happen when trucking elephants

The keeping system in elephant holding centres such as Pinnewala Elephant Orphanage in Sri Lanka and Elephant Conservation Centres (ECCs) in Sumatra are considered as "**alternative keeping systems**", which are intermediate between extensive and intensive. Elephants are allowed to live in family groups during the day and kept free or with hobbled front legs under close supervision of mahouts or range officers. Due to the limited foraging area and the risk of being injured by humans from nearby villages, they are not allowed free-range roaming at night, but are shackled or kept solitarily in small open or roofed areas. They are kept singly for a certain period of time during musth, or just before or after parturition, or during breaking procedures. A similar alternative keeping system is found in the Elephant Transit Home of the Uda Walawe National Park in Sri Lanka, where young elephants are kept in a semi-natural environment with minimal contacts with humans before they are brought back into the wild.

The daily amount and variety of activities are relatively high in elephants kept in the extensive system, but elephants kept in the intensive system are often idle. Stereotypies occur regularly. However, diverse daily activities exist in the elephants in the alternative keeping system, with limited or controlled interactions with other elephants. In most intensively kept populations, the age-sex structure is skewed towards either adults or infants, and towards one sex or the other, depending on the purpose of the elephants. For example, only sub-adult and adult bulls are used for religious festivals in Kerala, South India, while only infants, juveniles and females are used for tourism in the resorts of Thailand and India. Likewise, traditional and modern zoos and circuses use mainly middle-aged or old females and rarely include bulls or younger members. In contrast, extensively kept populations tend to have a more balanced age and sex structure (Kurt & Mar, 2003; Kurt *et al.*, in press).

1.3.2. The keeping system of captive Asian elephants in modern zoos

The term "modern zoos" in this thesis, refers to elephant holding facilities such as zoos as well as safari and wild animal parks in the Western hemisphere (Kurt & Mar, 2003). The current management systems in modern zoos can be defined as four different styles, known as Free Contact, Protected Contact, Confined Contact and No Contact (Figure 1.20), based on how keepers and elephants share the same work space (Clubb & Mason, 2002; Schmid, 1998a; Stevenson, 2002; Stevenson & Walter, 2006).

Free Contact is the management system, used by about 80% of zoos around the world (Clubb & Mason, 2002). This management system is derived from the intensive elephant keeping system, traditionally used in most Southeast Asian countries. Keepers and elephants share the same physical space. Keepers use negative and positive reinforcement to modify the behaviour of elephants. Keepers intentionally function in a position of social dominance within the elephant social hierarchy. Working with elephants in free contact is regarded as the highest risk occupation in North America (Lehnhardt, 1991).

There are accusations that taming and training involves physical punishment, especially in zoo elephants, because of the need to establish dominance over the elephant (Clubb & Mason, 2002; Haufellner *et al.*, 1993; Haufellner *et al.*, 1997). For the zoo management, the main disadvantage of Free Contact keeping is the dependence on qualified keeper staff (Haufellner *et al.*, 1993; Haufellner *et al.*, 1997) and tamed or tractable elephants (Schmid, 1998a). According to a 2003 interview by the Guardian newspaper with an elephant keeper from Blackpool zoo, UK, his salary was £230 a week. This low pay, coupled with high work load and the dangerous nature of the job leads to high staff turnover, and it can therefore be difficult for zoos to continue the tradition of keeping elephants in their exhibits (source: http://society.guardian.co.uk/publicvoices/story/0,,670326,00.html).

Keepers should have experience in training elephants, good knowledge of elephant behaviour, and a realistic and responsible awareness of the danger of working closely with these animals (Roocroft and Zoll, 1994. Some believe that continuous training enriches the elephants and makes them tractable (Schmid, 1998a). Elephants can be used for public entertainment, elephant riding and walks. The additional movement promotes the wearing down of soles and nails(Aava), supports the health of the circulatory system (Mill & Kuntze, 1978), and discourages obesity (Kurt & Pucher, 1996). There has been much debate on whether or not to keep elephants in Free Contact due to the high incidence of serious injuries to keepers during the late nineties (PETA, 2005). Among the recorded 122 elephant-inflicted accidents in modern zoos in the Western hemisphere between 1982 and 2004, 58% (n=71) of the total accidents were caused by elephants managed under the Free Contact keeping system (Gore *et al.*, 2006).

Protected Contact is the handling of an elephant when the keeper and elephant do not share the same unrestricted space. In this system, the elephant is not spatially confined and can move at will while the keeper stays on the other side of a barrier. Handling through a protective barrier is only possible if the elephants are trained to obey adequate commands. To educate the animals, Protected Contact requires qualified keeper staff in the same way as Free Contact management. Again, then, the zoo management depends on the availability of good elephant trainers (Clubb & Mason, 2002; Schmid, 1998a) and cannot guarantee the full safety of the handlers (Gore *et al.*, 2006).

Confined Contact is regarded as another kind of Protected Contact system; the elephant is handled or managed through a protective barrier, where the elephant is spatially confined, for example in an elephant restraining chute (ERC), which is built as a cage, where its movement its restricted. The elephant can be squeezed between the two sides of the cage, operated hydraulically. By tilting the walls sideways, an elephant in an ERC is forced into a laterally recumbant position, which is reported to be highly stressful to the animal in the chute, but is reported safe for elephant keepers.

No Contact keeping systems exclude all contact between people and elephants. This method is generally used for bulls, aggressive elephants and untrained, untamed elephants (Clubb & Mason, 2002). All the above-mentioned advantages of Free Contact keeping, which result from the possibility of contact with the animals and/or handlers, must be compensated for by adequate enrichment, to enable the animals to perform the majority of their natural behaviour patterns. In most parts of Europe it is not possible to keep elephants in outside enclosures throughout the year. Thus the requirements for an outside enclosure in No Contact management must be provided indoors as well. Another precondition for No Contact management is the keeping of well-socialized elephants in one group. Arbitrarily composed groups are not possible, because keepers cannot intervene in social conflicts (Clubb & Mason, 2002; Schmid, 1998a).

If all preconditions were met, No Contact keeping would have the advantage that the elephants were kept under nearly natural conditions. No elephant would be kept shackled for several hours daily. Trained keepers are not necessary in No Contact keeping; so the dependence on competent elephant personnel, and the difficulties of judging the relationship between keepers and elephants, do not exist for the zoo management.

In the wild, wear of feet and toenails mainly takes place during foraging, in the form of movements from one feeding place to another. It is impossible to meet this requirement in zoo enclosures, because most zoos cannot provide enough space for adequate roaming. No Contact keeping still needs human assistance in cases of veterinary intervention, such as radiography, nail trimming or assisted parturition. To do this elephants have to be anaesthetized or sedated (Bush, 1966), which is particularly risky in large animals (Fowler, 1995; Fowler, 2006b).

Since the publication of a review of zoo elephant welfare in Europe, commissioned by the Royal Society for the Prevention of Cruelty to Animals (RSPCA), UK, by Clubb and Mason (2002), zoos have been facing growing criticism of their elephant management programmes (Hutchings, 2006). Poor health and reproductive success of zoo elephants are the result of the combined impact of a lack of exercise, exposure to cold temperatures and disease, and stress due to brutal training techniques, chaining and inappropriate social environments. Many counter that zoo professionals strive to improve the standard of animal health and welfare so that every individual may live to the maximum life span for its species (Hutchins *et al.*, 2003).

Here in this thesis, I am particularly looking into the long-term effect of captivity on captive life span and reproductive potential of timber elephants living in an extensive keeping system, an environment which is equivalent to a mixture of free-contact living system (while working in timber extraction site) and no contact system (while foraging at nights) of zoo elephants. I explore in detail how capture and taming in combination with work-related stress act on their demography. I hope that the findings of my study will help to improve the welfare and performance of zoo elephants living in all management settings.

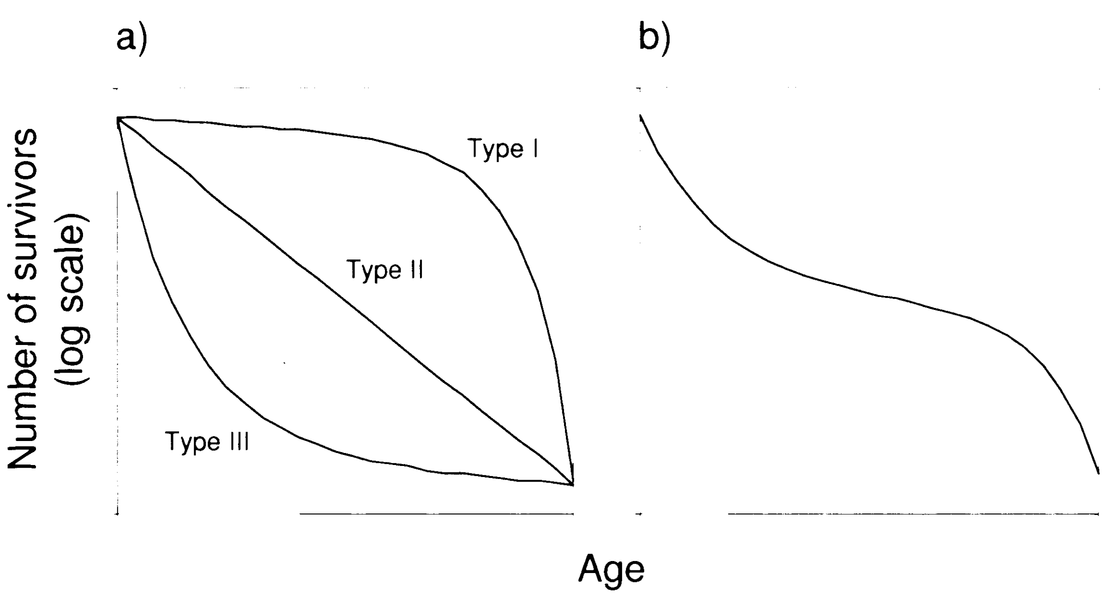
Figure 1.20. Four different elephant keeping systems in modern zoos

1.4. Life histories in long-lived species

The study of life-history strategies originated in the late 1940s and the early 1950s from the combination of animal demography and evolutionary theory (Heppell *et al.*, 2000). Traditionally, life history studies, used by many ecologists, focus on the interaction between age-specific survival probabilities and fecundities of an organism and its natural environment (Calder, 1984; Caughley, 1967; Partridge & Harvey, 1988; Partridge & Sibly, 1991; Sibly *et al.*, 1997; Stearns, 2000; Wikelski & Ricklefs, 2001). Studies of this kind are valuable in assessing the species' viability by estimating the effects of extrinsic and intrinsic factors on population change over time (Krebs, 1978; Stolen & Barlow, 2003).

An important tool in the study of life histories is the survivorship curve, where the probability of survival is plotted against age (Parmar & Machin, 1995). Raymond Pearl introduced three general types of survivorship curves (Figure 1.21, a) (Krebs, 1978; Pearl, 1922, 1927). Type I curves are from populations with very little loss for most of the lifespan and then high losses of older organisms, as they become senescent (Ricklefs & Scheuerlein, 2001). Diagonal (type II) survivorship curves imply a constant rate of mortality independent of age, while type III curves indicate high loss early in life, followed by a period of much lower and constant loss (Begon *et al.*, 1996; Krebs, 1978; Pearl, 1927). In reality, long-lived animals usually show a combination of these patterns (Figure 1.21b), with high mortality rates early and late in life, and low mortality in the middle years (Deevey, 1947; Krebs, 1978).

Figure 1.21. a) Hypothetical survivorship curves (after Pearl 1927) b) S-shaped composite survivorship curve typical of long-lived species



The underlying survival and reproductive rates that apply at each age throughout an organism's lifetime are frequently referred to as **life history characteristics** (Cole, 1954; Stearns, 1976, 1992). The life history characteristics are shaped by allometric scaling of various physical quantities, such as body weight, length, brain size and weight of offspring at birth, which can alter by their biological environment (May & Rubenstein, 1985). Body size is of fundamental importance to all considerations of physiology, ontogeny and longevity and has become a central issue in studies of mammalian life histories (Calder, 1984; Eberhardt, 1985; Millar & Hickling, 1991). Large size is reported to link with elevated extinction risk in mammals (Purvis, 2001) because larger species tend to exist at lower average population densities and they are disproportionately exploited by humans (Jerozolimski & Peres, 2003).

In the absence of predation or poaching, extrinsic factors that regulate the life history strategy of long-lived large-bodied mammals are food availability (Albon *et al.*, 1987; Altmann & Alberts, 2005; Bronson, 1995; Illius & O'Connor, 2000), population density (Clutton-Brock *et al.*, 1987a; Coltman *et al.*, 1999; Mysterud *et al.*, 2001; Solberg *et al.*, 2004), inter-and intra- group competition (Bercovitch & Strum, 1993; Bernstein, 1976), territoriality (Brotherton & Rhodes, 1996; Wolff, 1997), environmental "insults" (Gaillard & Yoccoz, 2003) such as extreme weather (Altwegg *et al.*, 2006; Murray *et al.*, 2006), chemical pollution (Crawford *et al.*, 2000), heat stress (Dyer *et al.*, 2007; Rey *et al.*, 2007), predation (Norberg *et al.*, 2006), poor husbandry practice (Asher *et al.*, 1996; Weladji & Holand, 2006) etc., disease (Cleaveland *et al.*, 2005; Randall *et al.*, 2006), and habitat loss and degradation (Barnes, 1999; Fernandez & Vrba, 2005; Leimgruber *et al.*, 2003; Sukumar, 2006). Additional factors such as overexploitation, invasive species, natural rarity, small geographic range, high tropic level or a combination of these can also affect their long-term survival leading to extinction (Mace & Balmford, 2000; Purvis *et al.*, 2000).

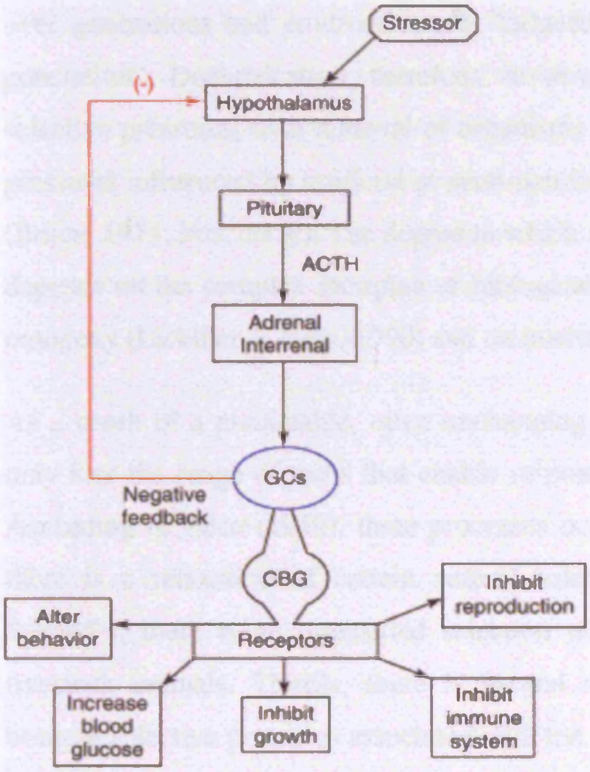
1.4.2. The effects of capture on life history

Various wild animals are captured for a range of reasons, particularly for help with work, and to enjoy as pets. This can cause acute stress and injury (Bailey *et al.*, 1996; DeNicola & Swihart, 1997; Grigor *et al.*, 1998), which affects life-history traits (Baenninger, 1995; Frankham, 2005b; Frankham *et al.*, 2002). When elephants are captured, they suffer capture effects at three different levels: (i) **Immediate effects** of capture, in which death can occur within a few minutes to a few hours after capture, known as per-acute deaths, may result from complications related to immobilization (respiratory depression, shock, hyperthermia, hyper- and hypotension, falling in a sternal position, falling with a limb in a malposition, asphyxia due to tympany or regurgitation), (Fowler, 1981; Fowler, 1995; Fowler & Mikota, 2006; Schmidt, 2003), or direct effects of capture operations such as strangulation by the rope or fettering chain while trying to noose or tie the wild elephant, or accidental injuries while driving them into a stockade, (ii) **Medium-term effects**, in which death may occur several days after capture (Arnemo *et al.*, 2006), may result from initally non-lethal injuries, such as pneumothorax due to misplacement of darts, infection from dart impact (Frankham, 2005a; Mikota *et al.*, 2003), trauma or infected wounds arising from traps and fettering chains and exertional myopathy from prolonged chasing (Schmidt, 2003), (iii) **Long-term effects,** where survival or reproductive rates may be reduced over the months or years following capture, may result from chronic stress or injuries related to training.

Physiological responses to capture-related stress are complex, and vary according to the nature of the stressor (Carlstead, 1996), age, sex, body condition and reproductive status of captives (Blas *et al.*, 2006; Jessop & Hamann, 2005; Perfito *et al.*, 2002) and restraint and handling time (Cattet *et al.*, 2003; Jones, 1977; Jones *et al.*, 2000; Ortiz & Worthy, 2000). The two most important physiological responses to stress in mammals are the stimulation of (i) the sympathetic nervous system and (ii) the hypothalamic-pituitary-adrenal (HPA) axis. At the initiation of a stress response, the sympathetic nervous system secretes norepinephrine from peripheral nerves and epinephrine from the adrenal medulla. These secretions promote glycogenolysis (the release of glucose from stored glycogen) and lypolysis (breakdown of fat) to initiate the fight-or-flight response. The HPA axis is activated simultaneously, with the release of corticotrophin-releasing hormone from the paraventricular nucleus of the hypothalamus, which triggers the anterior pituitary to release adrenocorticotropic hormone (ACTH), which in turn stimulates the cortex of the adrenal gland to release glucocorticoids (GCs). Glucocorticoids have multiple effects that are mediated by glucosteroid binding globulins (Figure 1.22). A negative feedback loop shuts off the HPA pathway leading to GC suppression. However, if the stressor persists and glucocorticoids remain elevated, negative feedback ceases to function and the deleterious chronic effects of glucocorticoids begin (Romero, 2004).

Figure 1.22. The hypothalamic–pituitary–adrenal (HPA) axis (after Romero, 2004)

Note: ACTH= adrenocorticotropin, GCs= glucocorticoids, CBG= corticosteroid binding globulins. Negative feedback is shown with a red line.



Physiologically, chronic stress accompanied with elevation of glucocorticoids can cause suppressed reproduction, suppressed immune responses (leading to poor wound healing and increased susceptibility to various diseases), reduced growth and loss of body condition due to reduction in protein synthesis in mammals (Munck *et al.*, 1984; Reeder *et al.*, 2004; Romero, 2004).

Behaviorally, chronic stress in animals and human may be indicated by reduced reproductive behaviour, increased abnormal behaviour, reduced exploratory behaviour and increased behavioural inhibition, increased vigilance behaviour and increased hiding, reduced behavioural complexity, increased aggression and increased fearfulness and frequency of startle responses (Carlstead, 1996; Carlstead & Brown, 2005).

1.4.3. Effect of captivity on life-history

According to Price (1984), domestication is defined as "a process by which a population of animals becomes adapted to man and to the captive environment by genetic changes occurring over generations and environmentally induced developmental events reoccurring during each generation". Domestication, therefore, involves an evolutionary process based on a shift in selective pressures, with removal of organisms from natural selection pressures to new selection pressures influenced by artificial or semi-natural environments and artificial selection by humans (Boice, 1973; Fox, 1978). The degree to which a wild animal is adapted for domestication largely depends on the complex interplay of biological, physiological and environmental factors during ontogeny (Lickliter & Ness, 1990) and on husbandry techniques (Price, 1984; Price, 1999).

As a result of a predictable, often unchanging environment in captivity, captured wild animals may lose the range of traits that enable responses to a variable and unpredictable environment. According to Price (1970), three processes occur during the process of domestication. Firstly, there is a relaxation of certain natural selection factors such as predation and starvation. Secondly, there is an intensified selection of traits preferred by humans, which is true for livestock animals. Thirdly, there is natural selection under captivity, leading to adaptation because selective pressures associated with the captive environment are vastly different from the native environment that species have previously inhabited (Hediger, 1964; Price, 1970).

Research has shown that captivity appears to have effects on the reproductive efficiency of captive animals, as determined by ages of puberty and senescence, seasonality of breeding, sperm production, ovulation rate, embryonic mortality, duration of pregnancy, litter size and lactational anoestrus (Klochkov *et al.*, 2005; Setchell, 1992; Setchell *et al.*, 2005), which are all subject to an individual's current phenotype and ambient external conditions (Taborsky, 2006)

Dependency on humans and domination by humans are thought to act as detrimental influences on temperament, survival and possibly reproductive performance in captive animals (Baenninger, 1995). For draft animals, timber elephants in particular, work–related stress may further increase the energetic burden of reproduction and their fitness.

1.4.4. Maternal effect on life-history

Parents play an important role with respect to growth rate, reproductive potential, behaviour and immune responses (Albon *et al.*, 1987; Allal *et al.*, 2004; Campbell & Dunkin, 1983; Shanks, 2002) of infants. Parental influence on their offspring can be through heredity (Kirkpatrick *et al.*, 1989) and through non-hereditary effects (Andersen *et al.*, 2000; Fisher *et al.*, 2006; Kirkpatrick *et al.*, 1989). Among parents, mothers are known to have the strongest non-hereditary influence on the life-history traits of their offspring (Altmann & Alberts, 2005; Kirkpatrick *et al.*, 1989). During the past few decades, many studies have focused on the role of the early developmental environment in the evolutionary process (Carter *et al.*, 2004; Scheiner, 1993a, b), focusing on relationships between maternal characteristics (e.g. diet, body size, social status, home range) and offspring life history characteristics later in life (Angilletta *et al.*, 2006; Charmantier & Garant, 2005; Charnov, 1989, 1990; Robbins *et al.*, 2007; Robbins *et al.*, 2004).

Mothers can influence the fitness of their offspring through resource provisioning, and offspring that are larger or emerge from larger propagules are generally more fit. For example, female red deer (*Cervus elaphus*) raised in a poor environment grow up with smaller adult size, lower energy reserves and inferior competitive ability, and produce smaller offspring with lower survival, resulting in significantly reduced life-time fitness (Albon *et al.*, 1986). The impact of adverse environmental conditions during the early developmental phase of the mother may be transmitted between generations by non-genetic maternal effects (Altmann & Alberts, 2005; Bateson *et al.*). In humans, studies have shown that a mother's condition, as determined by food deprivation, has strong long-term effects on offspring development and reproduction (Lummaa & Clutton-Brock, 2002a; Lummaa & Clutton-Brock, 2002b). Some studies show that this effect may even affect the third generation (Huck *et al.*, 1987). Here in this thesis, I will focus on non-hereditary maternal effects on life history characteristics.

1.5. Thesis structure

Analysis of the Burmese elephant studbook yields invaluable insights into patterns of fertility and mortality occurring under the prevalent management conditions. This information is equally relevant to research and to captive management. There is a general dearth of information on the long-term captivity of elephants placed into the extensive system. In this thesis, I document the demographic characteristics of elephants with different histories of captivity under work-related stress.

In Chapter 2, I present the basic demographic parameters and population changes over time of registered timber elephants in captivity. The life history analysis is based on the records of 8006 individually identified captive timber elephants employed for logging operations in Myanmar. Projected trends in population size and age and sex-specific structures, and life-table analyses, are conducted on captive-born and wild-caught elephant populations to predict the long-term sustainability of the population.

In Chapters 3-5, I explore the demographic factors underlying the patterns shown in Chapter 2. Chapter 3 investigates the factors affecting mortality patterns in working elephants (particularly age, sex and birth origin), and explores the causes of mortality. In Chapter 4, I explore the patterns and determinants of fecundity in captive elephants. The chapter focuses on reproductive output, inter-birth interval and birth sex ratio in relation to mothers' ages, parities and birth origins. In Chapter 5, I explore the short and long term effects of capture on the reproductive potential and survival probability of captive elephants mediated by maternal effects.

Finally, in Chapter 6, I briefly summarize the major findings of the previous chapters and address management implications and future research directions.

Chapter 2. Demographic parameters and population growth of working elephants in Myanmar

2.1. Introduction

As a long-lived mammal, elephants share many demographic traits with humans particularly in late age of sexual maturity, long gestation, single offspring and prolonged life-span (Connor *et al.*, 1998; Eisenberg, 1981; Leimgruber *et al.*, 2003). Some compare elephants' life history parameters to large-bodied long-lived marine mammals (e.g. odontocetes) particularly in cognitive ability, sexual size dimorphism, the delayed age of breeding, prolonged post-reproductive life span in females, low adult mortality but substantial infant mortality, prolonged duration of parental care and complex matrilineal-based societies (Connor *et al.*, 1998; Eisenberg, 1981; Roth & Dicke, 2005). An understanding of the key demographic parameters of elephants is essential for the conservation of the species.

Where sufficient life history data have been collected, large terrestrial mammals usually exhibit a characteristic pattern of age-specific death rates; (i) a juvenile stage with a low survival rate but increasing (survivorship curve concave) (ii) a prime-aged middle life, with relatively high and stable rates of survival (curve more or less straight) and (iii) an old or a senescent stage with a decreasing survival rate (curve convex) (Caughley, 1966; Caughley, 1977; Deevey, 1947; Eisenberg, 1981; Kerten, 1953). This pattern is so common that its absence is usually thought to indicate defects in the data (Caughley, 1966; Spinage, 1972).

Life tables of large mammals such as hippopotamus (Laws, 1968), African buffalo (Sinclair, 1977), Himalayan thar and Dall's sheep (Caughley, 1966; Caughley, 1977), African ungulates (Spinage, 1972), bears (Freedman *et al.*, 2003) and marine mammals (Stolen & Barlow, 2003) have been derived from the age-at-death data. Several of these studies utilized carcasses, skulls, dentition or similar artifacts to determine the ages of the animals (Laws, 1968; Sinclair, 1977; Spinage, 1972). Some use photo-identification (Barata & Brooks, 2005; Kelly, 2001; Meekan *et al.*, 2006; Mizroch *et al.*, 2004; Moss, 2001), visual identification through individual marking such as hot-ironed, freeze and chemical branding (Hindell, 1991; Lay *et al.*, 1992; Schwartzkopf-Genswein *et al.*, 1997), individual physical characteristics (Altmann & Alberts, 2005), radiocollar (Marshal *et al.*, 2006) and ear tag and/or ear tattoo (Birgersson & Ekvall, 1997; Marker *et al.*, 2003) for identification of individuals to estimate annual survival rates. Here in this study, permanent branding with its unique registration number is used for identification of individual animals.

Early studies of demography on African elephants (*Loxodonta africana*) were largely based on carcass examinations of individuals shot as part of culling operations taken either at a single point in time (Laws *et al.*, 1975) or on a regular basis (Hall-Martin, 1984), through aerial counts (Douglas-Hamilton, 1972; Hall-Martin, 1984, 1992) and visual estimates (Moss, 1996; Moss & Poole, 1983; Poole *et al.*, 1997). Most of these studies rely on assumptions and projections to describe the population's history and predict its future trends (Armbruster & Lande, 1993). Only a few studies of elephants have actually followed a population in detail, and even these only over a short period of time (Douglas-Hamilton, 1972; Hall-Martin, 1984, 1992; Weyerhauser, 1982; Whitehouse & Hall-Martin, 2000). Examples of successful, detailed, long-term studies are few due to logistical, financial and other constraints, Moss's (2001) long-term study of a population of individually known, free-ranging African elephants in Amboseli National Park, Kenya being one exception.

Published data on the demography of Asian elephants (*Elephas maximus*) are mostly focused on wild populations (McKay, 1973; Nair, 1980,1978; Santiapillai *et al.*, 1984; Balakrishnan, 1986; Sukumar, 1998,2003; de Silva, 1995, 1997; Sukumar & Santiapillai, 1996; Easa, 2002; Katugaha *et al.*,1989; Vidya & Sukumar, 2002). By comparison, very few reports on captive Asian elephant populations are published, due to the lack of reliable records extending back several decades (Das, 2003; Gopinath, 1990; Joy, 1990; Mahasavangkul, 2001; Sukumar *et al.*, 1997). The current study seeks to redress both these gaps by providing a demographic study of individually-identified captive Asian elephants over a 48 year period. Specifically, this chapter aims to (a) document the population structure of the Myanmar captive elephant population over the last five decades and (b) to develop a cohort life table for timber elephants of two different birth origins, namely captive-born and wild-caught, in order to determine whether the captive timber elephant population is self-sustaining in the long term.

2.2. Materials and methods

2.2.1. Data selection

The captive elephants discussed in this study are owned by the government of Myanmar, and employed at the Myanma Timber Enterprise (MTE) and the Forest Department under the jurisdiction of the Ministry of Forestry. I had access to a record of 8006 elephants born and captured between 1910 and 2000. However, about a third of these records lack complete information on dates of birth and loss to follow up, and are excluded from the analyses. Although there are 8006 elephants in the studbook, the total number of elephants use for analysis of this chapter is 5292 (total captive-born population=3131, male=1527, female=1562; total wild-caught population=2161, male=766, female=1395), 98% of them born or captured since 1950.

2.2.2. Life-table analysis

The life history is a set of data which is usually summarized in the form of a life table (Bell, 1980), containing age-specific reproductive and survival rates (Brommer, 2000; Muller *et al.*, 2004). This table is derived from counts of the numbers of individuals alive in the population at each age, together with the numbers of births to mothers in each age class. The raw data isc derived from ages at entry, departure and parturition, and I, therefore use a cohort (or vertical) life-table approach (Caughley, 1966; Caughley, 1977; Deevey, 1947; Krebs, 1978). Calving data contains extensive information on mothers (e.g., mothers' date of birth, mothers' birth origin etc.); it is impossible to get paternal data because most calves are sired by wild male elephants during free roaming/foraging at nights. As the potential growth rate of the population is my main interest, my model contains only female segment, assuming that population growth depends the quantity and distribution of reproduction through the life history (Bell, 1980).

The columns of the life-table are made up of the following components:

f_x **(the total number of individuals alive at age x)** is calculated by subtracting the number of deaths, escapes, transfers and censors (those still alive at the end of the study period or otherwise lost to follow-up at a known date) between the ages of x-1 and x (e_{x-1}) from the number of survivors at the previous age (f_{x-1}), and adding the number captured over the same period (c_{x-1}):

$f_x = f_{x-1} + c_{x-1} - e_{x-1}$

$\boldsymbol{q_x}$ **(age-specific mortality rate)** is the proportion of animals alive at age x that die before age $x+1$ and is calculated as the number of individuals in the cohort that died between the ages of x and $x+1$ (d_x) divided by numbers alive at age x (f_x):

$$q_x = \frac{d_x}{f_x}$$

$\boldsymbol{l_x}$ **(age-specific survivorship)** is the probability at birth of surviving to exactly age x:

$l_x = l_{x-1}\,(1 - q_{x-1})$

$\boldsymbol{m_x}$ **(age-specific fecundity)** is the average number of female offspring produced by an individual female aged between x and $x+1$, calculated as the number of female live births (b_x) divided by the approximate mid-year population of mothers M in the age class:

$$m_x = \frac{2b_x}{M_x + M_{x+1}}$$

From these columns, the following life-history values can be calculated:

$\boldsymbol{R_0}$**, (net reproductive rate)** is the average number of daughters produced by each female in the population over the course of her lifetime. It is obtained by multiplying together the l_x and m_x schedules and summing over all age groups:

$R_0 = \sum l_x m_x$

In field studies, R_0 is used to measure lifetime reproductive success (Clutton-Brock, 1988; Newton, 1989, 1995).

***T*, (generation time)** is the average age at which a female first produces young. It is calculated as:

$$T = \frac{\sum x l_x m_x}{R_o}$$

***r_0*, (intrinsic rate of increase or the Malthusian parameter)** is the instantaneous rate at which the population increases. Net reproductive rate and generation time together determine the rate of growth of populations; the higher the reproductive rate and shorter the generation time, the greater the intrinsic growth rate of a population (Gaillard *et al.*, 2005):

$$r_0 = \frac{\ln R_o}{T}$$

Net reproductive rate (R_0) is regarded as the multiplication rate per generation while, intrinsic rate of increase (r_0) is the *per capita* instantaneous rate of increase per time unit of a population with a stable age distribution (Brommer, 2000; Cole, 1954).

λ (finite rate of population change) is the net rate of change over a given time interval, in this case one year, indicating whether the population is increasing ($\lambda > 1$) or decreasing ($\lambda < 1$). It is calculated as:

$$\lambda = e^{r_0}$$

Percent population change per year is calculated as: $100^* (\lambda - 1)$

In calculating age-specific fecundity, female calves born to mothers with full information on their survival and fecundity are used. If females are found with missing information on birthing records (e.g., calving date, parity, sex of calf), both females and their calves are excluded from the analysis. Population pyramids, (i.e. comparing the age structures of captive-born and wild-caught living populations) are presented as percentages of the total population. Analyses were performed using Statistical Package for Social Studies (SPSS) Release 12.0 (SPSS Inc., Chicago, USA).

2.3. Results

2.3.1. Observed population growth rate

The number of elephants entering the recorded population initially increased over time, but decreased slightly in the 1990's (Figure 2.1). Over this period, the balance of entries to the population shifted strongly from capture to birth. As a result of this pattern of captures, the size of the recorded population steadily increased from 1960 to 1995 and then remained roughly stable until the end of study period (Fig. 2.2a), while the representation of wild-caught elephants initially increased up to the mid-1970's, followed by a decline (Fig. 2.2b). In every year, females dominated the population structure (Figure 2.2c). The degree of female bias was greatest around the 1980s, following the peak of capture activity, and reflecting a preference for females in capture operations (see below). Births and deaths both increased as the known population increased, but births declined more recently while deaths continued to increase as the known population aged (Figs. 2.1 & 2.3).

Figure 2.1. Total births, deaths and captures by decades

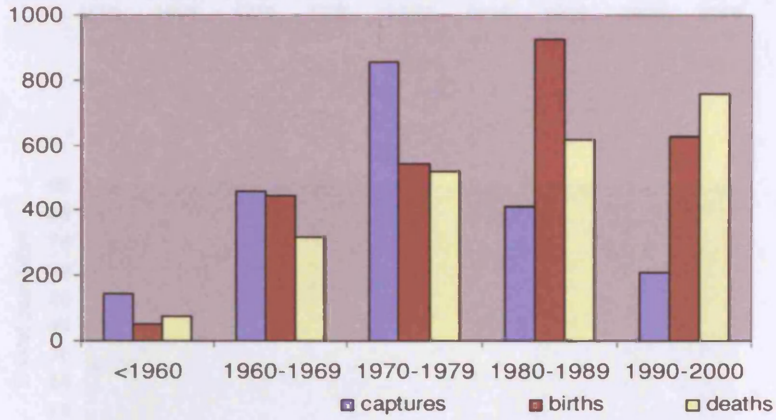
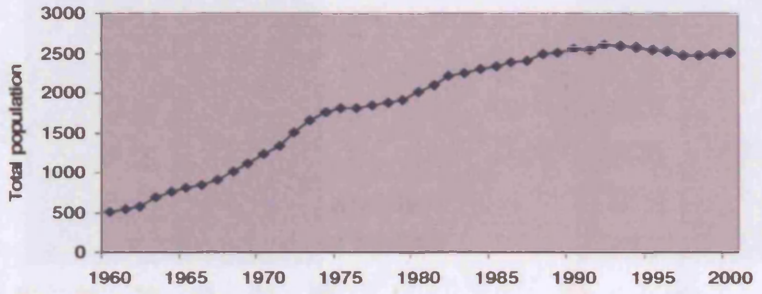
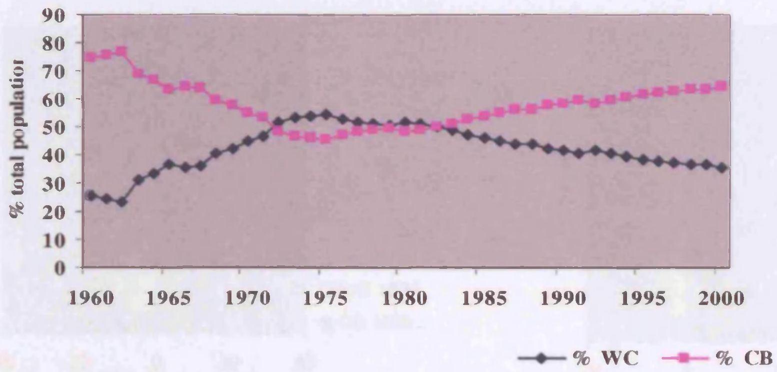


Figure 2.2. Changes in the size and structure of the recorded population over time, representing animals recorded in the data base with full life-history details (not the actual numbers in the population) (a) Numbers recorded in the population; (b) birth origin structure WC: wild-caught, CB: captive-born; (c) sex structure

(a)



(b)



(c)

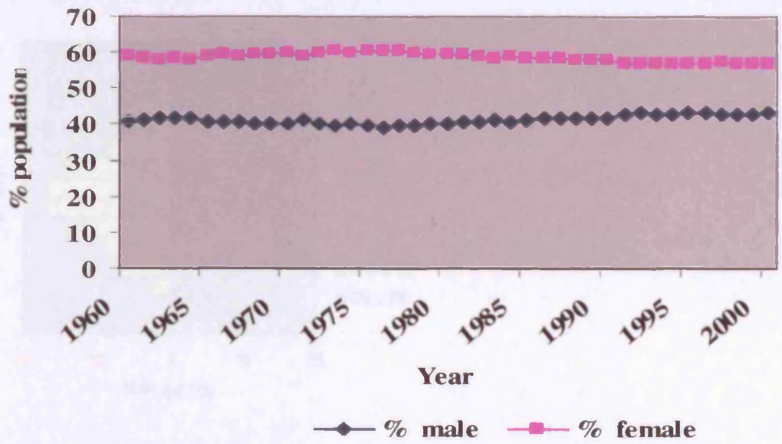
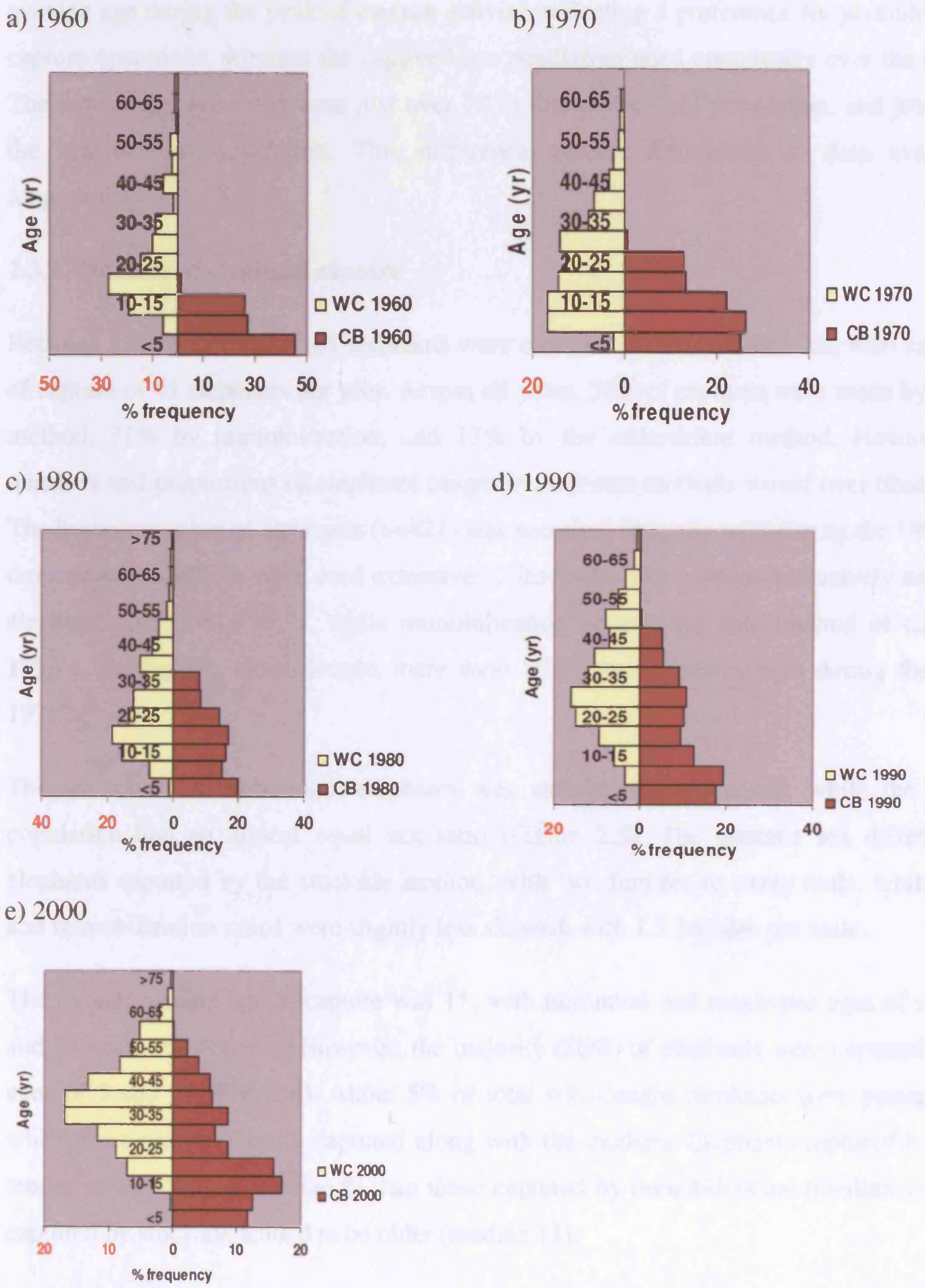


Figure 2.3. Age structure in the recorded populations of wild-caught and captive-born elephants at ten year intervals. WC: wild-caught; CB: captive born.



The age structure of the population was initially extremely biased towards juveniles and infants, but aged progressively over time (Fig. 2.3). Wild-caught elephants showed an initial decline in average age during the peak of capture activity, reflecting a preference for juvenile elephants in capture operations, whereas the captive-born population aged continually over the entire period. The oldest ages observed were just over 79 in the wild-caught population, and just under 60 in the captive-born population. This difference reflects differences in data availability, not longevity.

2.3.2. Patterns of elephant capture

Between 1952 and 2000, 2161 elephants were captured alive from the wild, with an average rate of capture of 45 elephants per year. Across all years, 56% of captures were made by the stockade method, 31% by immobilization, and 13% by the milarshikar method. However, the total numbers and proportions of elephants caught by different methods varied over time (Figure 2.4). The highest number of elephants (n=821) was recruited from the wild during the 1970s, when all three capture methods were used extensively. Stockades were almost exclusively used to capture elephants until mid 1980's, while immobilization became the sole method of capture by the 1990's. During this latest decade, there were 80% fewer captures than during the peak in the 1970's.

The sex ratio of wild-caught elephants was strongly female-biased, while the captive-born population had an almost equal sex ratio (Figure 2.5). The greatest sex difference was in elephants captured by the stockade method, with two females to every male, while milarshikar and immobilization ratios were slightly less skewed, with 1.5 females per male.

The overall median age at capture was 11, with minimum and maximum ages of seven months and 67 years respectively. However, the majority (56%) of elephants were captured between the ages of 5 and 20 (Fig. 2.6). About 5% of total wild-caught elephants were younger than five, which were unintentionally captured along with the mothers. Elephants captured by milarshikar tended to be younger (median 8) than those captured by immobilization (median 9), while those captured by stockade tended to be older (median 13).

Figure 2.4. Changes of population structure of wild-caught elephant population by different capture methods by decades

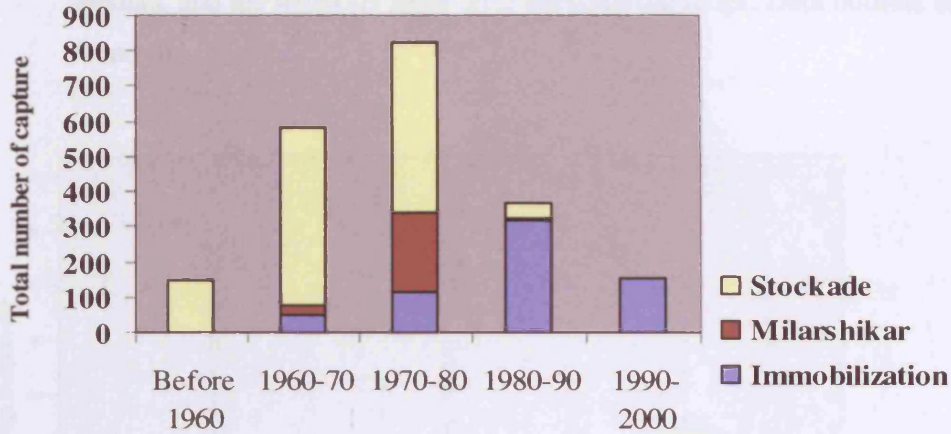


Figure 2.5. The sex ratio of wild-caught elephants, split by capture method, compared with captive-born elephants

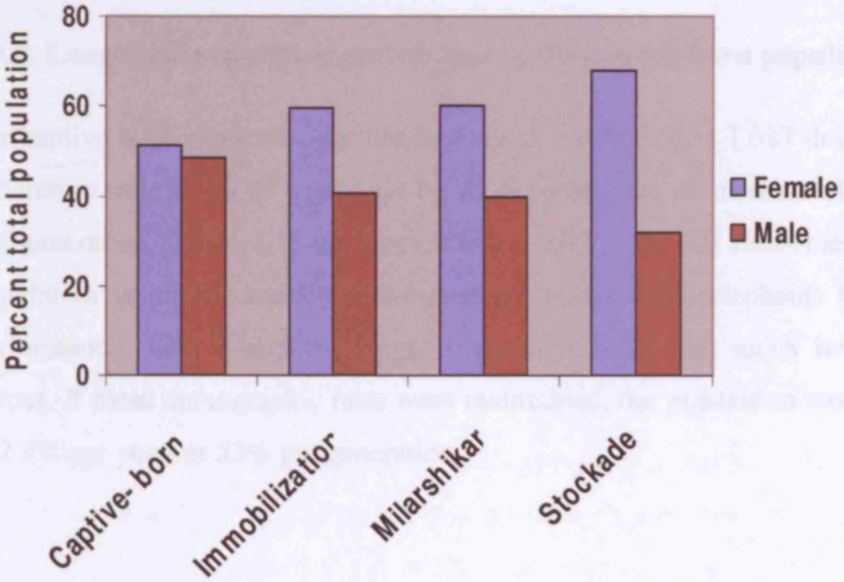
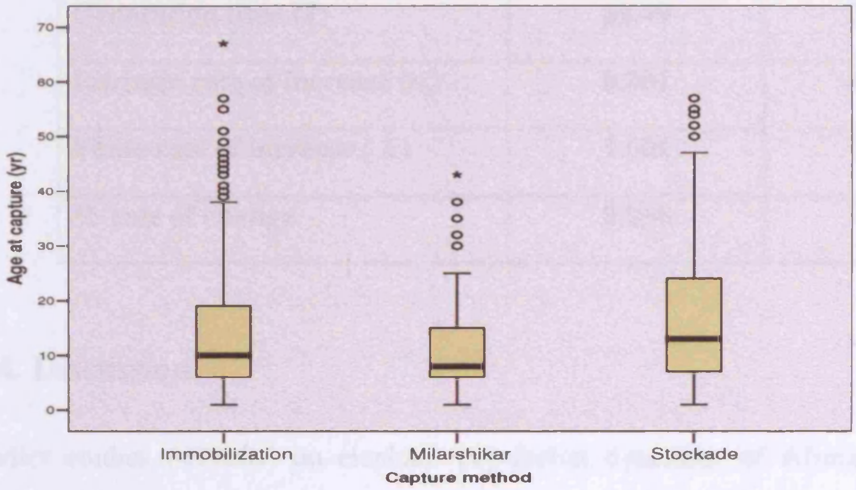


Figure 2.6. Box-and-whisker plots of capture age of wild elephants by capture methods (Note: The box shows the interquartile range, the middle line depicts the median, and the whiskers show ±1.5 interquartile range. Data outliers are also shown as * and o)



2.3.3. Long-term population growth rate in the captive-born population

For captive-born elephants, the net reproductive rate (R_0) is 1.017 daughters per mother, with a generation time of 29.49 years, giving an expected rate of increase of 0.06% per year, or 1.7% per generation (Table 2.1, see Appendices 1 and 2 for full life-tables). This indicates that the population is almost exactly self-replacing. Wild-caught elephants have poorer demographic performance, with a slightly longer generation time, and much lower lifetime reproductive output. If these demographic rates were maintained, the population would be expected to decline at 2.3% per year, or 53% per generation.

Table 2.1. Population growth parameters based on cohort life tables for captive-born and wild- caught elephants.

	Captive-born	Wild- caught
Net reproductive rate (R_0)	**1.017**	**0.477**
Generation time (T)	**29.49**	**32.33**
Intrinsic rate of increase (r_0)	**0.001**	**-0.023**
Finite rate of increase (λ)	**1.001**	**0.977**
% rate of change	**0.056**	**-2.26**

2.4. Discussion

Earlier studies (<1960s) on elephant population dynamics of African elephants was mostly estimated by death and birth rates (Hanks & McIntosh, 1973), indicating that population density was the major population regulatory factor (Laws & Parker, 1968) because field researchers have noted that elephant birthrate varies with densities (Buss & Savidge, 1966) and crowded populations experienced lower fecundity and higher mortality (Laws, 1969a; Laws, 1969b). Several approaches have been used to estimate the elephant populations. The "life table approach" was used (Caughley *et al.*, 1994) from naturally dead elephants where aging was estimated from dentition (Laws, 1968, 1969b) while others used the same methodology by observing living known-age animals (Douglas-Hamilton, 1972; Moss, 1988; Moss, 2001).

This study is based on a captive Asian elephant population that has not been significantly affected by poaching or culling. The population change over time will reflect the patterns of births, deaths and captures if the biodata on individuals were accurately compiled over time, however during the early years of this study, a full record of the population was not available. Full and accurate records on the vast majority of individuals were available from around 1950. Thus by the 1990s, the elephants recorded in this study would have comprised the vast majority of the individuals alive at that time. As a result, while the initial increase in the size and average age of the recorded population primarily reflects the accumulation of records in the database, the population age structure and trend in the late 1990s are likely to be accurate reflections of the population as a whole.

From the early 1990s to the end of the study period, the population of timber elephants was roughly stable, totaling between 2500 and 2700 (Figure 2.2,a). The proportion of wild-caught elephants in the population declined from the 1970s onwards (Figure 2.2,b) because of decreasing capture in later decades, which culminated in the Myanmar government's "no capture" policy, which was officially declared in 1995. Because capture was phased out, the population structure in 1990 (Figure 2.3,d) and at the end of this study (Figure 2.3,e) showed an ageing wild-caught sub-population with the highest proportion (≈30%) within the older (>35 yr) age group. Meanwhile, more than half of the captive-born population at the end of the study lay in the juvenile and sub-adult group under 20 years of age, indicating a healthy birth rate within the captive population (Fig 2.1), which was contributed by both captive-born and wild-caught females. Taking account of an increasing number of captive-born elephants in the reproductive age class between 15-30 years at the end of study period, the MTE population is expected to grow in the future without capture from the wild.

During the past decade, demographic studies have been done on free-ranging wild African (Lewis, 1984; Moss, 1996; Moss, 2001; Wittemyer *et al.*, 2005) and Asian elephants (Sukumar & Santiapillai, 1996; Easa, 2002; Katugaha *et al.*,1989; Vidya & Sukumar, 2002). There have also been demographic studies on a few zoo populations (Weise, 1997; Weise & Willis, 2004) and in some captive Indian elephant populations (Easa & Sabu Jahas, 2002; Nair, 1980; Saseendran *et al.*, 2002). Sukumar et al. (1997) have presented an unusually detailed demographic study of captive elephants from the state-owned forest timber camps in the Tamilnadu State of Southern India, which was kept in a keeping system similar to my study population. The elephants were able to socialize with captive con-specifics during day time and with wild elephants while they were let out to forage at night. Based on 417 adult elephants known to be alive between 1969 and 1989, they reported the intrinsic growth rate (r_0) and annual population growth of South Indian captive timber elephant population as 0.005 and 0.5% per annum, respectively, commenting that the captive elephants in South India could be self-sustaining or even showing an increasing trend in the absence of capture. They also suggested that availability of wild bulls for siring calves and a lower work load than in previous years due to official banning of logging in the whole India might contributing to a high birth rate. Likewise, captive elephant population in Thailand is believed to be stable, because most elephants are engaged in the light work of carrying tourists in eco- and urban- tourisms (personal communications, Dr. Preecha Phaungkum).

Here, in this study, I separately presented the population trends of the captive-born and wild-caught elephants of MTE. Similar to the South Indian captive population, the captive-born sector of the MTE timber elephant population was also self-sustaining. In contrast, although wild-caught MTE elephants had a similar generation time to the captive-born sector (captive-born=29.5 versus wild-caught=32.3), the wild-caught sub-population showed a negative intrinsic rate of increase. Because the captive-born population is only just self-sustaining, if any future increase in population is required, it will be necessary either to re-instate a capture policy, which would not be accepted by the global conservation community, or to find ways of improving captive breeding. This will require a detailed understanding of the factors determining survivorship and fecundity, which are covered in the following chapters.

2.5. Conclusion

The growth rate of the captive population is expected to improve in future decades, because the sex ratio is strongly female-biased, and the number of sexually mature females can be expected to increase. On the other hand, ever-increasing logging burdens and forest thinning might limit the ability of adult females to get enough forage to maintain body reserve. As stated by Bronson (1989) the food supply is the single most important environmental variable controlling mammalian reproduction. For any population, an organism's innate capacity for increase depends on its fertility and longevity, which again varies with age and under the influence of resource availability. If Myanmar officials do not capture from the wild to recruit working elephants, they will have to boost age-specific fecundity rates by providing nutritional supplementation and reducing the work load to prevent work-related stress. A secondary goal should be to reduce mortality rates in all age groups.

Chapter 3. Mortality patterns of working Asian elephants of Myanmar

3.1. Introduction

Although long-term data on age- and sex-specific survival are difficult to obtain in long-lived large-bodied species, limited information on survival exists for large mammals in the families Ursidae (Freedman *et al.*, 2003; Garshelis *et al.*, 2005; Hellgren *et al.*, 2005; Lazar *et al.*, 2004; Sorenson & Powell, 1998), Elephantidae (Hanks & McIntosh, 1973; Laws & Parker, 1968; Laws *et al.*, 1975; Lee & Moss, 1995; Moss, 2001; Sukumar *et al.*, 1997), Pongidae (Doran-Sheehy & Boesch, 2004; Dunbar, 1980; Hill *et al.*, 2001; Johnson, 2003a; Mace, 1988), Otariidae (Le Boeuf & Reiter, 1988), Delphinidae (Arndt & Swadling, 2006; Connor *et al.*, 1998) and Hominidae (Hawkes, 2003; Hill & Hurtado, 1989; Kennedy, 2005). Apart from *Homo sapiens*, most of these demographic studies on large mammals are snapshots of a sub–set of the population in one location, focusing on the effects of age and sex on survival, usually in juveniles, prime-aged and senescent adults (Caughley, 1966).

Most studies focus on wild populations (Balakrishnan & Easa, 1986; de Silva *et al.*, 1995; Easa & Sabu Jahas, 2002; Ishwaran, 1993; Katugaha *et al.*, 1999; Kurt, 1974; Leimgruber *et al.*, 2003; McKay, 1973; Nair, 1978; Santiapillai *et al.*, 1984; Sukumar, 1989b; Sukumar & Santiapillai, 1996; Vidya *et al.*, 2003). Demographic reports on captive elephant populations are fewer; most of them are based on the studbook data of captive zoo elephants in Europe (Belterman, 2001; Clubb & Mason, 2002; Dorrestyn & Terkel, 2000), North America (Hutchins & Smiths, 1999; Keele, 1997, 1999; Keele, 1998) and Australia (Peper-Edwards, 2005). Although elephants have a long history of being tamed and raised as beasts of burden in the range states of Asia (Csuti, 2006; Delort, 1992; Sukumar, 2003a), there is a dearth of scientific literature on the long-term effects of captivity on survival and fecundity, due to the lack of reliable records that can be traced back several decades. Previous studies of demographic rates in captive Asian elephant populations, whilst informative, have been based on relatively small sample sizes (Faust *et al.*, 2006; Sukumar *et al.*, 1997; Weise, 1997, 2000; Weise & Willis, 2004), thus limiting the scope of questions that could be addressed. Studbook data of logging Asian elephants of Myanmar are particularly suitable for the study of age- and sex-specific mortality and fecundity patterns because each individual elephant has been given a unique registration number and its dates of birth, capture and death are known.

In this chapter, I will analyze age- and sex-specific survivorship of the world's biggest captive Asian elephant population. The major aims of these analyses are:

(1) to quantify the age- and sex-specific survival differences of wild-caught and captive-born elephants

(2) to explore survival differences of wild-caught elephants by capture methods

(3) to present the etiology of mortality.

3.2. Materials and methods

3.2.1. Study population

As cohort survival analysis is used throughout this chapter, only elephants with known dates of birth or capture and death or last confirmed existence are included. Stillbirths and elephants of unknown sex are also excluded. Excluded records were mainly from before 1950, when record-keeping was less consistent and precise, although a small number of more recent records showed errors in data recording or transcription through date of death being earlier than date of birth or capture. These records were also excluded. The sub-set of the data used for analysis was filtered systematically step by step from the original studbook, as stated in Table 3.1.

Table 3.1. Selection of elephants for survival analysis from the studbook data (The full data set contained 8006 records)

Step	Sample	n	Total remaining in the filtered data
1	Dates of capture shown only to the nearest decade before 1950	1674	6332
2	Dates of birth or death missing	1037	5295
3	Date of death < date of birth or capture	85	5210
4	Stillbirths, premature births and abortions	101	5109
5	Unknown sex	1	5108

The study population allows me to study life history biodata of elephants for a maximum of four generations. After excluding incomplete records, the total elephants remaining for survival analysis are 5108, in which 56.9% are females and 43.1% males. Having excluded the number of elephants captured before 1950s, sub-set of filtered data contain wild-caught elephants (n=499) with estimated age at the time of capture that born during the late eighteenth century, with the earliest estimated date of birth at 1895 (elephant registration number = 87, name = Mo Ra Na, was captured in 1952 at the estimated age of 57). The earliest data entry date for captive born elephants in the entire data set is recorded as 08/12/1925 (the date of birth of elephant registration number 1843 (name=Sa Bae). Although I fix the end of the study period at 31/12/2000, the actual study period spans for more than a century (approximately 105 year), taking account the fact that the earliest recorded (estimated) date of birth at 1895 for wild-caught elephant. Among 5108 elephants, the total number of elephants that died during the study period is 2159 (Table 3.2).

Table 3.2. Cross-tabulation of the timber elephant population by sex, origin and fate

Birth Origin	Total number	Female	Male	Total
Captive-born (n=3032)	**Total elephants that died**	**566**	**673**	**1239**
	Living population	**996**	**797**	**1793**
Wild-caught (n=2076)	**Total elephants that died**	**577**	**343**	**920**
	Living population	**767**	**389**	**1156**
Total population in the filtered data		**2906**	**2202**	**5108**

For the under-five age group, only calves born in captivity with complete information on birth order, death date, birth date and mother's birth origin, are chosen for survival analysis and the variables of interest are sex of calf, birth origins of mother, parity and mother's age. Among the remaining calving records (n=2503), 704 calves (male=386, female=318) died before they reached the age of five. I create separate models for the survival analysis of elephants aged over five, with variables of interest birth origins and sex. For this analysis, the age bracket is set between five (before which there are very few wild-caught individuals) and 55 (there are very few individuals older than this in the data set, particularly captive-born). One thousand four hundred and eighty one elephants (male=622, female=859) died before 55 during the survival analysis study period.

The definition of the age classes in elephants varies somewhat between authors (Lee & Moss, 1999; Mikota *et al.*, 1994; Sikes, 1971; Sukumar, 1989a). Here I use the term 'calves' for the under-five age group (age range 0 to 5yr), sub-adult for the 5 to 25 age group, and adult for elephants older than 25.

3.2.2. Methods

I use survival analysis to test hypotheses about differences in survivorship between groups. In such analyses, the variable of interest is "*time until event occurs*", in this case, the age at which death occurs. An initial step in the analysis is to present graphical summaries of the survival trend for individuals in the pooled population. Such summaries act as a precursor to a more detailed analysis of the data set. Date of departure from the population is defined by either death, escape, theft or transfer to a different, unmonitored population, or the end of the study period, the latter possibilities representing right censoring of the data (i.e. departure without event occurrence). For captive-born elephants, the study period starts at the date of birth, so that observations are right-censored only. By contrast, wild-caught elephants enter the study population at various ages, meaning that a variable portion of the early history is not observed, and data for these individuals are therefore both left- and right-censored.

Survivorship or survivor function and hazard ratio or hazard function are two quantitative terms which will be used extensively in the future chapters. The survivorship gives the probability that an individual survives longer than specified time. It is a fundamental to a survival analysis, because obtaining survival probabilities for different values of specified time, commonly denoted as ***t***, provides crucial summary information from survival data. Theoretically, as ***t*** ranges from 0 up to infinity, the survivorship can be graphed as a smooth curve. In practice, when using actual data, it is usually visualized as steps, rather than smooth graphs. Through a modeling approach to the analysis of survival data, it is possible to document how the survival function depends on the values of one or more explanatory variables and to demonstrate the potential influence of explanatory variables on survival time (Kleinbaum, 1996).

The hazard function or hazard ratio gives the instantaneous potential per unit time for the event to occur, given that the individual survived up to the specified time. In contrast to the survivor function, which focuses on ***not failing***, the hazard function focuses on ***failing***, that is, on the event occurring. Thus, in some sense, the hazard function can be considered as giving the opposite or negative side of the information given by the survivor function, which means that the higher survivorship function for a given or specified time, the smaller the hazard function and is vice versa. The hazard function is sometimes termed as conditional failure rate (Kleinbaum, 1996)

There are several methods available to analyze time-to-event curves, such as Cox proportional hazards, log-rank, and the Wilcoxon two-sample test, for example. Here, I use the Cox model, a regression method for survival data that provides an estimate of the hazard ratio (an estimate of the ratio of the hazard rate between explanatory variables, where hazard rate is the instantaneous risk of death) and its confidence interval, and allows the effects of several risk factors on survival to be analyzed simultaneously. The Cox model allows hazard rates to vary with time, but assumes that the rates at different levels of explanatory variables are proportional to one another. Where non-proportionality is detected, data are separated into shorter age ranges both to avoid false conclusions caused by non-proportional hazards, and to identify where differences lie in the age range. Independent variables, with the exception of mothers' age, are treated as time-constant covariates.

Survival analyses and tests of the proportional hazards assumption are determined by using the survival library of the free statistical software package 'R' (version,1.9.0, released 2004-04-12, web address: http://cran.r-project.org/). A significance threshold of $\alpha = 0.05$ is used. Minimum adequate models are found by removing the variables with the least significance level sequentially from the full model until only significant variables remained.

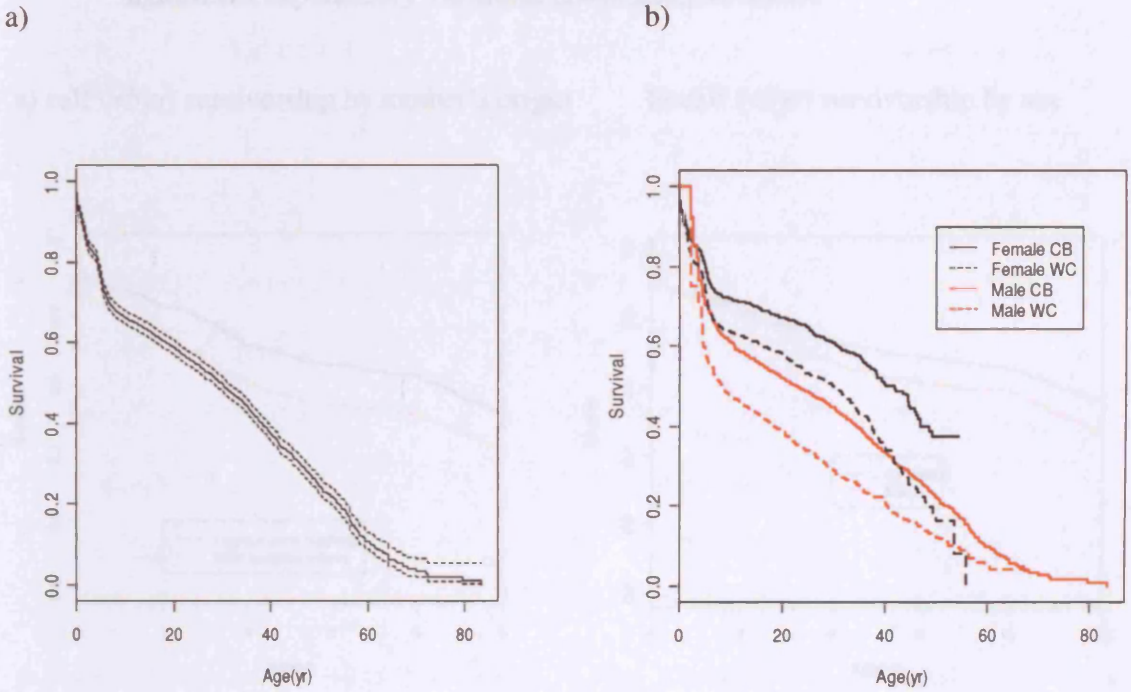
3.3. Results

3.3.1. Determinants of mortality

The survival curve for elephants across all ages is S-shaped, Type 2 survivorship graph, as stated in Figure 1.23 (Figure 3.1, a). The mortality rate is high in the early years, with one third of the total population dying before they reach their 10th birthday (survival to age ten = 0.66 ± 0.01 SE). Mortality then reduces in the middle years, increasing again in later life with senescence.

Sex and birth origin both have significant independent effects on survivorship (Figure 3.1,b), with males and wild-caught elephants having significantly higher mortality rates than their counterparts. The hazard functions of males and females remain proportional throughout their life span (Cox proportional hazards test $\chi^2 = 0.48$, $P = 0.49$). However, the Cox proportional hazard test indicates that survival curves for wild-caught and captive-born elephants are strongly non-proportional ($\chi^2 = 5.87$, $P<0.05$). This partly reflects the apparent lack of mortality in wild-caught elephants aged less than five, which is due to lack of data, as very few elephants were captured before the age of five.

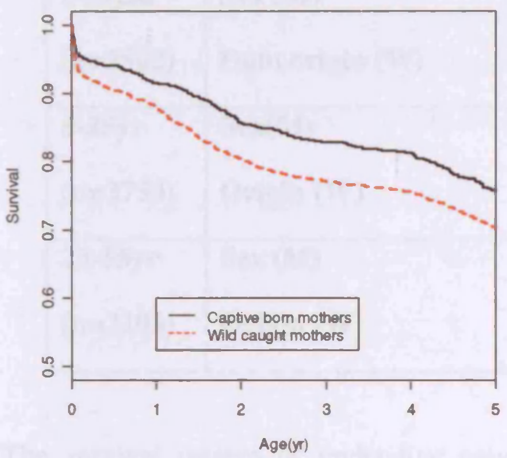
Figure 3.1. Survival of elephants in the population as a whole (a), and compared between sexes and birth origins (b) (CB=captive- born, WC= wild- caught) Figure 3.2.



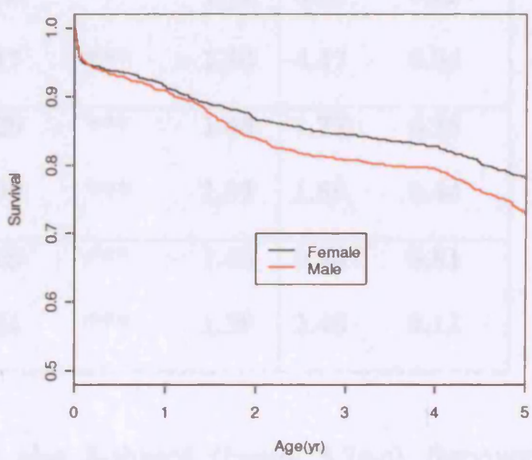
Lack of proportionality between the survival curves of different birth origins makes the significance tests above unreliable, and it is therefore necessary to repeat these tests for narrower sections of the age range within which mortality rates are proportional between groups. Hazard functions are found to be proportional in three age groups, which are under-five, aged between 5 and 25 and aged between 25 and 55 (Figure 3. 2 and Table 3. 3).

Figure 3.3. Survival curves for elephants in different age groups, illustrating significant explanatory variables (F=female, M=male)

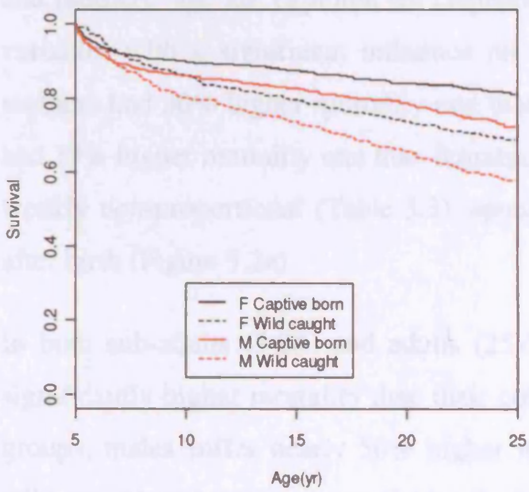
a) calf (<5yr) survivorship by mother's origin



b) calf (<5yr) survivorship by sex



c) sub-adult (5-25yr) survivorship



d) adult (25-55yr) survivorship

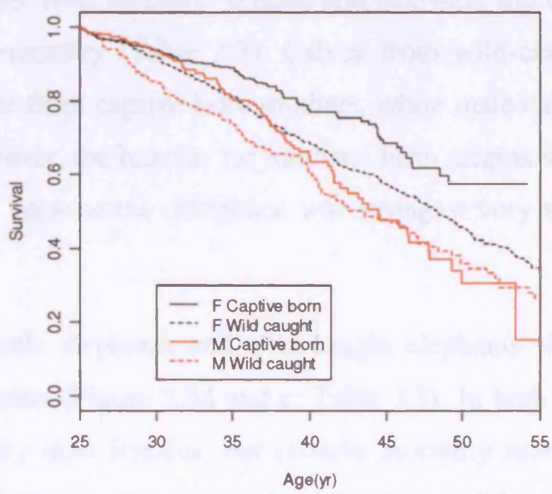


Table 3.3. Test results for differences in survival by sex, birth origins, parity, mother's age and different age groups (M = male, W = wild-caught, Z = text statistic, P = probability, e^{β} = exponential coefficient, level of significance *** = P<0.001 and * = P<0.05)

Age range (total)	Variables	Cox regression			Proportionality	
		Z	P	e^{β}	χ^2	P
0-5year	**Sex (M)**	**2.20**	*	**1.19**	**0.25**	**0.62**
(n=2502)	**Dam origin (W)**	**3.17**	***	**1.30**	**4.47**	**0.04**
5-25yr	**Sex(M)**	**5.29**	***	**1.48**	**1.77**	**0.18**
(n=3753)	**Origin (W)**	**7.94**	***	**1.87**	**1.59**	**0.44**
25-55yr	**Sex (M)**	**4.68**	***	**1.48**	**0.56**	**0.81**
(n=2103)	**Origin (W)**	**3.61**	***	**1.39**	**2.48**	**0.12**

The survival pattern of under-five calves is also S-shaped (Figure 3.2a-c). Survivorship (± standard error) at the end of the first year of life is 0.90 ± 0.01, indicating that the first year mortality rate is ≈ 10%, and over a quarter of calves born alive died before they reach their fifth birthday. When the relationship between survival and sex, birth order of calf, mothers' origins and mothers' age are explored for elephants under five, mothers' origins and sex were the only variables with a significant influence on calf mortality (Table 3.3). Calves from wild-caught mothers had 30% higher mortality rate than those from captive-born mothers, while male calves had 19% higher mortality rate than females. However, the hazards for mothers' birth origins were weakly non-proportional (Table 3.3), apparently because the difference was strongest very soon after birth (Figure 3.2a).

In both sub-adults (5-25) and adults (25-55), male elephants and wild-caught elephants show significantly higher mortality than their counterparts (Figure 3.3d and e; Table 3.3). In both age groups, males suffer nearly 50% higher mortality than females, but relative mortality rates in wild-caught and captive-born elephants differs between age groups. In sub-adults, wild-caught elephants have a mortality rate 87% higher than captive-born, whereas in adults, they differ by only 39% (exponential coefficients 1.87 versus 1.39).

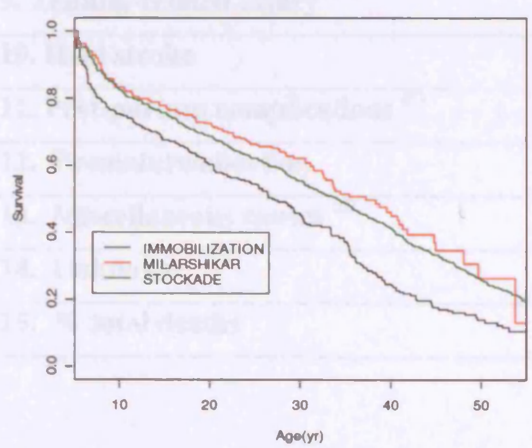
3.3.2. Effect of capture methods on survival of wild-caught elephants

Wild elephants were captured using one of three different methods. Among these, animals captured by immobilization show the lowest survival rate (Figure 3.3, Table 3.4), with a mortality rate 38% and 25% greater than animals captured by milarshikar and stockade respectively. When the survival analysis is separately conducted to compare milarshikar and stockade methods, animals captured by the stockade method have about 12% higher mortality rate than those captured by milarshikar, however this difference is not significant (χ^2 = 1.65, p=0.10).

Table 3.4. Comparisons of models for survival rates by capture methods (Z = text statistic, P = probability, e^β =exponential coefficient, level of significance *** = P<0.001)

Capture methods	Cox regression			Proportionality	
	Z	*P*	e^β	χ^2	*P*
Milarshikar	**3.62**	***	**0.62**	**0.05**	**0.83**
Stockade	**3.29**	***	**0.75**	**0.07**	**0.79**

Figure 3.4. Survivorship curves for wild-caught elephants, split by capture methods



3.3.3. Causes of death

Of the total deaths, 79.49% recorded the causes of death (Table 3.5). Death due to accidents (25.97%) and general weakness (13.07%) are the most frequently cited of the known etiologies. Accidents are more prevalent in younger elephants (<5yr) while general weakness (see definition in Table 3.5) is more common in older elephants aged over ten. Failure to produce enough milk in females (mother agalactia) is the second most common cause of death in the under-five age group. In general, there are no obvious differences in death causes between sexes (Figure 3.4) except that more females (7.74% versus 5.28%) die of general weakness and more males die of diseases (4.77% versus 3.84%) and of parasite infestation (4.45% versus 3.98%).

Table 3.5. Cause of death in elephants by age group

Death causes	Age			Total
	<5yr	5-25yr	25 +yr	
1. Accidents [1]	10.79	9.54	5.63	25.96
2. General weakness [2]	2.79	5.63	4.65	13.07
3. Diseases[3]	3.44	3.21	2	8.65
4. Gastrointestinal worms and liver flukes	1.95	4.84	1.67	8.46
5. Mother agalactia	7.49	0.14	0	7.63
6. Gastrointestinal complications [4]	1.26	2.04	0.98	4.28
7. Killed for ivory	0.28	2.09	0.7	3.07
8. Old age	0	0	2.3	2.3
9. Taming-related injury	1.35	0.97	0.05	2.37
10. Heat stroke	0.28	0.65	0.74	1.67
11. Post-partum complications [5]	0	0.28	0.49	0.77
12. Premature/abortion	0.32	0	0	0.32
13. Miscellaneous causes [6]	0.23	0.52	0.19	0.94
14. Unknown	2.47	10.6	7.44	20.51
15. % total deaths	32.7	40.6	27.12	100

Notes:

1. Accidents include falls from higher ground, occupational injuries, falls into a ravine or river, attacks by wild elephant or tiger, trauma/injuries inflicted by older sibling for competition of milk, drowning, lightning strikes, snake bite, strangulation on chains, choking, forest fire /quicksand and hit by train.

2. "General weakness" represents a nutrition-related unexplained wasting condition that cause exercise intolerance and failure to perform the standard norm of dragging efficiency by the age set by Departmental regulations (see detail in Chapter 1).

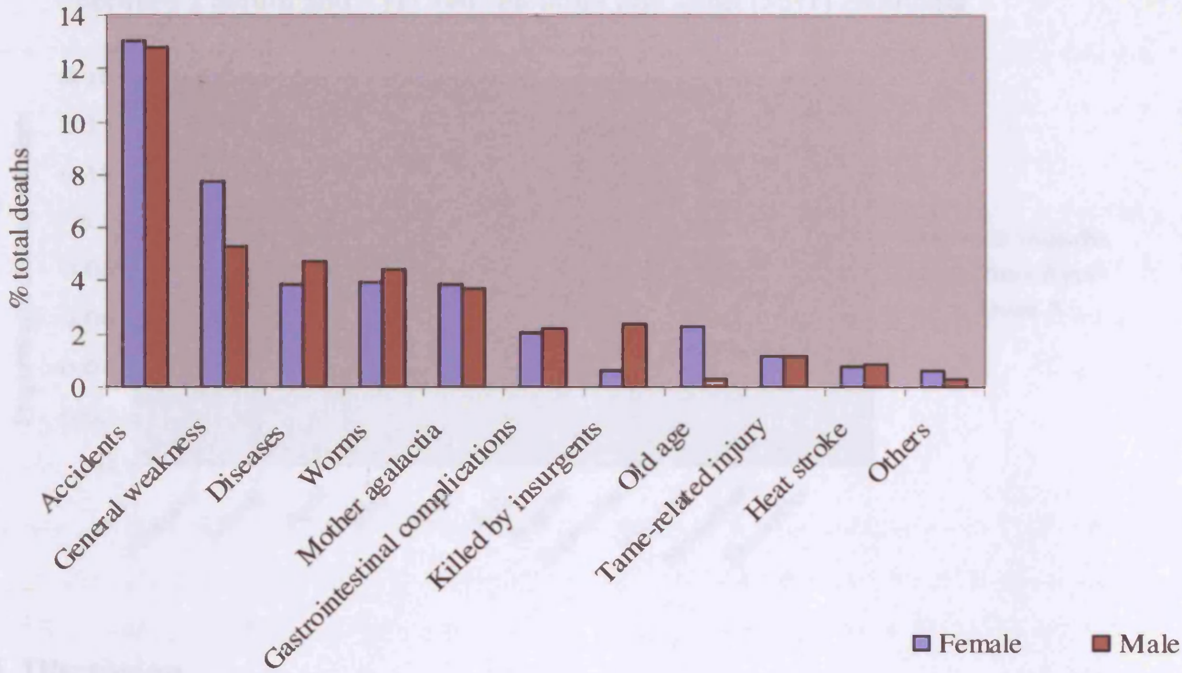
3. Diseases due to infectious agents such as foot and mouth disease, tetanus, rabies, rinderpest, anthrax, hemorrhagic septicemia; rabies, trypanosomiasis, pneumonia, lung infections and tuberculosis. Today's commonly known viral infections such as endotheliotropic herpesviruses, encephalomyocarditis etc are not reported in the Studbook data as it is likely that these diseases are not well-studied or under-reported during the study period between 1925 and1999.

4. Gastrointestinal complications are constipation, diarrhea, over feeding, enteritis, colic and bloat

5. Post-partum complications include uterine prolapse, retention of foetal membranes, rejection by mother, killing by mother

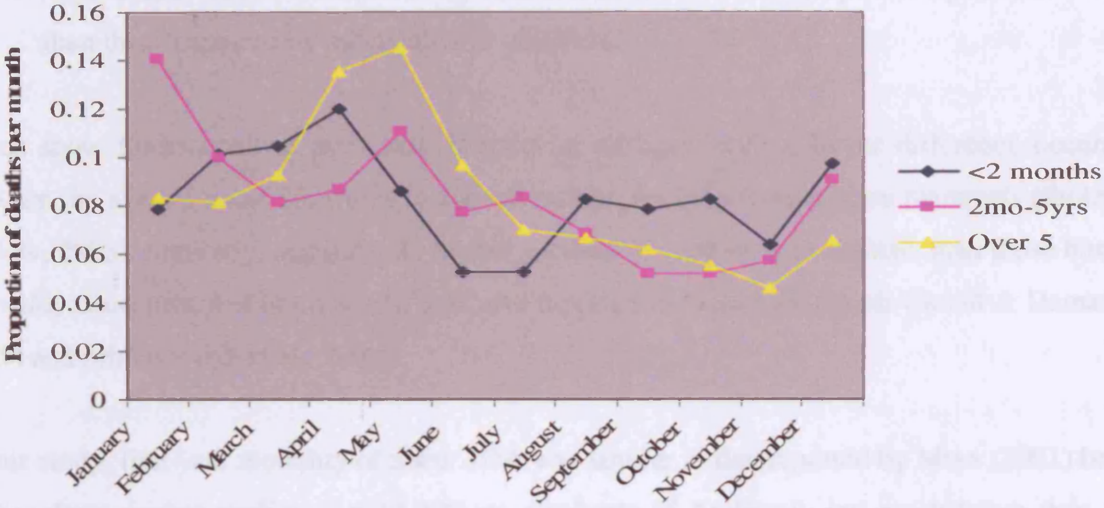
6. Miscellaneous causes include musth-related problem, food-poisoning, salmonellosis, poisoning, hernia, wound etc.

Figure 3.5. Causes of death in male and female elephants



There was significant seasonal variation in mortality in elephants older than five (χ^2 = 179.3, p < 0.0001), and in calves between two months and five years ($\chi^2{}_{11}$ = 47.4, p < 0.0001), but not in neonates ($\chi^2{}_{11}$ = 14.9, p = 0.18) (Figure 3.5). A high death rate is observed in the hottest months (from April to May), especially in adults (Figure 3.5). Adult mortality declines in the rainy season, which is June to October, and in the cool months of October and November and then mortality slightly increased in December, which was likely related to the third stage of timber extraction (details in Chapter 1, Methods of utilization of elephants in timber industry), which normally took place in the end of the year. Calves aged between two months and five years show peak mortality in January.

Figure 3.6. Monthly variation of mortality of neonates (<2mo.), juvenile (aged between 2 month and 5 yr) and sub-adult and adult (>5yr) elephants



3.4. Discussion

3.4.1. Overall survivorship pattern

The overall survival curve for timber elephants was similar to survival curves observed in studies of other large-bodied, long-lived terrestrial (Sinclair, 1977; Spinage, 1972) and marine mammals (Barlow & Boveng, 1991; Stolen & Barlow, 2003) and humans (Fergany 1971; Juckett & Rosenberg, 1993; Muehlenbein & Bribiescas, 2005; Pinder III et al., 1978). Looking more closely at different age classes, survival analysis of calves (under 5) showed the following characteristics:

In calves born alive, 10% died before their first birthday, and 27% died before their fifth birthday. Male calves and calves born to wild-caught mothers showed higher mortality than their counterparts.

Accidents and agalactia (lack of or deficient milk formation) in mothers were the most common causes of calf mortality.

Survival analysis of sub-adults and adults (5-55) showed the following characteristics:

1. Accidents and general weakness were the most common causes of death.
2. Males suffered a higher mortality rate than females.

3. Wild-caught elephants suffered a higher mortality rate at all ages, but less so in older elephants.
4. Wild-caught elephants captured by immobilization showed comparatively lower survival than those captured by milarshikar or stockade.

Males show lower survival rates than females at all ages, with a larger difference occurring between the ages of 5 and 25, which is not uncommon for long-lived marine mammals (Stolen & Barlow, 2003). Similarly, significantly higher survival of captive-born animals than those born in the wild, as documented in my study, was also reported in marine mammals (Small & Demaster, 1995) and primates (Ha et al., 2000).

In this study, first year mortality of about 10% was similar to that reported by Moss (2001) based on her demographic studies of wild African elephants of Amboseli, but much lower than that reported in intensively kept zoo elephants, with an estimated first year mortality of about 30% in North American (Keele, 1998; Weise, 2000) and European zoos (Clubb & Mason, 2002; Kurt & Mar, 1996; Schmid, 1998b). However, first year mortality of timber camp elephants in South India was estimated at 24% for female, because less care was given by owners/mahouts due to lower economic value/return than bull and 16% for male calves (Sukumar *et al.*, 1997), intermediate between this study and zoo populations.
I suggest that there are four major risk factors leading to the mortality pattern reported in this chapter:

1. Nutrition
2. Climate
3. Male physiology
4. Capture, taming and work- related stress

3.4.2. Nutrition as a risk factor

According to the allometry of metabolism, elephants have lower nutrient requirements per unit of body weight compared to smaller herbivores (Owen-Smith, 1988), so that they need prolonged foraging time or supplementary feeding if they have limited foraging time, to meet their physiological needs. Digestive physiology of mature Asian and African elephants' resembles that of horses but their digestive tracts are surprisingly short compared to other herbivores (Clauss *et al.*, 2003a; Clauss *et al.*, 2007; Loehleim *et al.*, 2003); as a result, elephants have faster passage rate of ingesta and the absolute digestibility coefficients achieved for all nutrients are distinctly lower than other herbivores (Clauss *et al.*, 2003b). Hackenberger (1987) and Clauss and associates (2007) showed that Asian elephants, which are grazers (taking a higher proportion of grass in their diet) need longer ingesta retention than their African counterparts, which are browsers (preferring twigs, branches etc.). Similar difference in digestive efficiencies are reported in browsing rhinoceros (*Diceros bicornis*) and grazing rhinoceros (*Ceratotherium simum* and *Rhinoceros unicornis*) (Clauss *et al.*, 2006; Clauss & Hatt, 2006). As Asian elephants prefer grass and/or bamboo, flexible materials that do not break easily require longer time to get fermentation (Hummel *et al.*, 2006a; Hummel *et al.*, 2006b), assuming that Asian elephants need sufficient time for foraging and for digestion.

While the elephants in my study received supplementary feeding, it is likely that inadequate time for foraging and digestion played a role in the mortality patterns observed. First, for animals used for draught, sport or recreation, inadequate nutrition is one of the major factors that affects their survival, reproduction and draught power because their energy requirements are higher than those of non-working animals (Lawrence, 1990; Pearson & Dijkman, 1994) and a higher intake level should be expected to balance energy requirements. For example, the extra energy intake in draft cattle increases up to 1.8 times maintenance levels, and in horses up to 2.4 times (Pearson & Dijkman, 1994). In working elephants, the intake of paddy or paddy straw increases almost twofold during the logging season compared to the non-logging seasons (Kaushik, 1999), however, this may be insufficient for some groups of animals. Lastly, as a grazer, timber elephants may need sufficient time for fermenting and digestion.

While the elephants in my study received supplementary feeding, it is likely that inadequate nutrition played a role in the mortality patterns observed. First, for animals used for draught, sport or recreation, inadequate nutrition is one of the major factors that affects their survival, reproduction and draught power because their energy requirements are higher than those of non-working animals (Lawrence, 1990; Pearson & Dijkman, 1994). For example, the extra energy intake in draft cattle increases up to 1.8 times maintenance levels, and in horses up to 2.4 times (Pearson & Dijkman, 1994). In working elephants, the intake of paddy or paddy straw increases almost twofold during the logging season compared to the non-logging seasons (Kaushik, 1999), however, this may be insufficient for some groups of animals.

In particular, males incur greater energy costs, in many sexually dimorphic species (Clutton-Brock *et al.*, 1987a), but also in the case of working elephants because they are given greater timber–hauling tasks than females. Given competition for the best forage during free foraging, it may be that some males struggle to meet this increased energy demand.

Wild-caught elephants also tend to have unfavourable energy budgets due to reduced food intake, especially during the early years in captivity, because of capture-related stress, failure to compete with captive-born resident elephants in accessing good forage, and unfamiliarity with the locality. Access to high-quality feeding grounds and local familiarity are important for foraging and survival, and can improve with residence time in an area (Part, 2001). Furthermore, animals of low social status generally have low food intake (Lee, 1996; Lee *et al.*, 1991) and thus attain sub-optimal body condition in adult life, giving birth to small infants and/or producing inadequate lactation to meet the needs of their offspring (Barker, 1998). It is therefore likely that depression of nutritional status is responsible for reduced survival observed in both wild-caught elephants themselves, and in their offspring.

Nutritional factors probably also play a role in the reduced survivorship seen in calves around the age of four to five. This is the age at which calves make the transition to a fully solid food diet, which entails some risk. Unlike most herbivorous mammals, digestion in adult elephants takes place in the caecum and colon (Hatt & Clauss, 2006), whereas calves rely on the fore-gut. During weaning, gut morphology and digestive physiology gradually change to a hind-gut digestion process (Clemens & Maloiy, 1982), and failure to make this transition efficiently, while selecting appropriate solid foods, can lead to inadequate nutrition and elevated mortality risk. It may also be that the increase in mortality at this age is influenced by the onset of training, which can result in reduced feeding, and occasionally potentially fatal injuries.

Numerous researches in human and farm animals have shown that when born too early, their digestion and thermoregulation system were not fully developed. Such infants are at risk for increased perinatal mortality, birth adaptation complications, including perinatal acidosis, hypoglycemia, hypothermia, coagulation abnormalities and susceptible to various diseases due to immunologic deficiencies (Burrin *et al.*, 1992; Chardon *et al.*, 2006; Herpin *et al.*, 1994; Kasari, 1994; Nowak, 2006; Pallotto & Kilbride, 2006). In humans, studies have shown that breast feeding helps prevent hypothermia and hypoglycaemia in newborn babies (Huffman *et al.*, 2001) because many hormones such as growth hormone releasing hormone, gonadotropin-releasing hormone, thyrotropin-relerasing hormone etc, growth factors and bioactive substances were present in mothers' colostrums (Buhimschi, 2004; Ebrahim, 1996), suggesting that breastmilk has a role in the further development and maturation of the immune system of the newborn. Peaked mortality of elephant calves under two months in cool months of December and January (Figure 3.5) in my study, is likely born premature or those born to mothers with poor lactating ability, so that their deaths seemed due to one or compounded with lactation-related and/or inadequate growth/development of major organs in premature or underdeveloped calves that lead to hypothermia and respiratory related infections.

3.4.3. Climate as a risk factor

High solar radiation, high ambient temperatures, a lack of water and cover and unpredictable food and water resources challenges thermoregulation and water balance in large animals (Cain *et al.*, 2006). Changes in exposed surface area, circulation or fat reserve can all be used to change insulation and ultimately control heat exchange (Phillips & Heath, 1995). The low surface-to-volume ratio and apparent absence of sweat glands (except for interdigital glands) has raised numerous questions regarding how elephants maintain thermal balance (Fowler, 2006a). Elephant's ears are regarded as an important part in regulating their body temperature, as there are many blood vessels in the ear. Ear flapping can cool down the body temperature (Benedict, 1936; Sikes, 1971). Temperature regulation in large animals is slower than smaller ones and they regulate heat loss by decreasing surface temperatures (McNab, 1983; Phillips & Heath, 1995) . Elephants decrease their body temperature by wallowing in river/stream/mud to wallow, by drinking large amount of water and by staying in shady place (Forthman, 1998).

Temperatures in Myanmar frequently exceed 40 degrees Celsius in April and May, and mortality in adults peaked during these hottest months of the year. There are two likely reasons for this.

First, there is a lack of sufficiently nutritious forage during the hot season, which might sharpen the nutritional problems discussed above. Second, there may be direct effects of heat stress. Heat stress is a potentially fatal syndrome threatening the central nervous system and multiple organ dysfunction (Sucholeiki, 2005). Working elephants in Myanmar are rested during the hottest months in order to avoid this risk, however it may be that even resting elephants are at risk of heatstroke when temperatures are extremely high. Calves (<5yr) showed some tendency to higher mortality in the hot months, but much less so than in adults. This may be due the fact that their thermoregulatory system is less developed than adults, enabling them to cool off more effectively.

In older calves, peak mortality occurred in the coolest month of the year (January). However, even at this time of year temperatures in Myanmar are usually moderate, and the same mortality peak is not seen in neonates, which would be expected to be more vulnerable to chilling. It is therefore unlikely that the January mortality peak is caused by low temperatures. A more likely explanation is that training of older calves mostly takes place in the coolest months of the year, and training-related injuries and depressed nutrition are therefore responsible for this peak in mortality (Chapter 1, Taming method for details)..

3.4.4. Male physiology as a risk factor

Survival and mating success are key fitness components of mammalian males. While many studies have examined fitness trade-off in females, there are limited studies on trade-offs faced by males (Pelletier *et al.*, 2006). In theory, male traits that confer a mating advantage bear survival disadvantages (Clinton & Le Boeuf, 1993). Studies on wild ungulates have shown that rutting is costly (Jorgenson *et al.*, 1997; Mysterud *et al.*, 2005). Likewise, in my study, healthy male elephants sporadically show the phenomenon of musth, a hormone-mediated condition associated with increased aggressiveness, restlessness and reduced feeding activities from about the age of ten (Dickerman *et al.*, 1997; Eisenberg *et al.*, 1971; Jainudee *et al.*, 1972; Poole & Moss, 1981). During musth, males undergo significant weight reduction, progressive loss of body condition and increased inter-male aggression associated with markedly elevated androgen and cortisol levels. This phenomenon is extremely stressful, both psychologically and physiologically (Brown *et al.*, in press). Musth may last from one day up to several months in captive and wild

Asian (Dickerman *et al.*, 1997; Jainudee *et al.*, 1972; Rasmussen & Perrin, 1999) and African elephants (Hall-Martin, 1987; Poole, 1987; Poole & Moss, 1981), during which they may lose up to 10% of their total body weight (Rasmussen & Perrin, 1999). This loss of condition, combined with increased aggression leading to higher risk of injury, is likely to lead to increased mortality risk in male elephants undergoing musth.

3.4.5. Capture and taming stress as risk factors

While nutrition was mentioned above as a possible factor in the elevated mortality risk observed in wild-caught elephants, there is also likely to be a direct impact of capture and taming in this group. Fear has been widely regarded as a powerful and damaging stressor (Jones, 1977). Sudden, unpredictable, intense, prolonged, inescapable fear and distress combined with social disruption of the natal group during capture, followed by breaking and training, are highly stressful for freshly-caught elephants. Exposure to a physical or psychological stressor produces a host of acute and chronic physiological changes, such as reduced immune function, cardiovascular insufficiencies, and alterations in hormonal production (e.g. concentrations of adrenalin or cortisol). These stressors might also lead to the development of abnormal behaviours (Korte, 2001; Mostl & Palme, 2002; Reeder *et al.*, 2004; Romero, 2004), and ultimately to reduced reproductive output and longevity. Capture stress may also interact with nutritional factors, as some reports indicate that survival of wild-caught animals is diminished when body condition is below a threshold (Roffe *et al.*, 2001).

Risk of mortality appears to vary according to capture method, which suggests that not only is captivity and training damaging, but that the act of capture itself can be more or less risky. Surprisingly, survival was highest among elephants captured by the milarshikar (noosing) and stockade methods, while the immobilization method resulted in the lowest survival probability. When elephants are captured by stockade, females are mostly caught, along with their related kin. As a result, stockade elephants receive kinship support during the post-capture period and they seem to suffer less stress in captivity than those captured by milarshikar or immobilization, the methods selectively chosen for young sub-adult individuals. However, the majority of the effect is probably due to higher risk factors involved in immobilization. By comparison with immobilization operations in other large mammals, these factors are probably a combination of injuries from falling as the drug takes effect, and physiological problems resulting from adverse reactions to, or incorrect dosages of, drugs (Cattet *et al.*, 1997; Kock *et al.*, 1995; Portas, 2004).

3.5. Conclusion

This study produced several important results. In this chapter, I have documented that the first-year survival rate was 90%, but 27% of live-born calves died before their fifth birthday. Male calves, first-born calves and calves born to wild–caught mothers show significantly lower survival rate than their counterparts whereas, among sub-adults and adults (aged between 5 and 55), wild–caught male elephants show higher mortality than their counterparts. Malnutrition, heat-stress and lack of quality forage in summer, musth, and capture, taming and work-related stress were major risk factors incorporated in the mortality pattern of both calf and adult timber elephants. Capture method has a profound impact on mortality patterns with animals captured by the immobilization method having higher mortality than those captured by stockade or milarshikar methods.

Chapter 4. The determinants of fecundity and birth sex ratio in female timber elephants

4.1. Introduction

Large, long-lived mammals fall into the category of '*K-selected*' species that exhibit slow life histories, with low levels of fecundity, delayed attainment of puberty and decreased mortality (Rachlow & Berger, 1998). Reproductive success in these species has been shown to respond to many different factors, including seasonal availability of food resources (Altmann & Alberts, 2005; Sibly & Hone, 2002), predation (Zager & Beecham, 2006; Zanette et al., 2006), adult survival rate (Pistorius *et al.*, 2004; Schaub *et al.*, 2006), population density (Owen-Smith, 2006; Rachlow & Berger, 1998), social factors (Alados & Escos, 1992; Archie *et al.*, 2006; Garcia *et al.*, 2006; Vervaecke *et al.*, 2005), group sex ratio (Holand et al., 2003), ecological, psychological or physiological stress during early development (Festa-Bianchet *et al.*, 2000; Gunn *et al.*, 1995; Shanks, 2002) or a combination of these factors (Bradshaw *et al.*, 2002; Coulson *et al.*, 2001). For captive females, reproductive success can be further influenced by confinement-related stress (O'Regan & Kitchener, 2005; Smith & Chavey, 1993; Wielebnowski, 2003), capture-related trauma and stress (Alibhai *et al.*, 2001; Frankham, 2005b), inadequate space, housing and enrichment (Hutchinson, 2005; Rennie & Buchanan-Smith, 2006; Shepherdson, 1989), adverse environmental conditions (Harthoorn, 1979; Wielebnowski, 2003), failure to provide compatible breeding pairs or social groups (Barnett *et al.*, 1986; Watts & Meder, 1996), frequent changes in group composition (Clubb & Mason, 2002; Schulte, 2000), inability to train animals properly (Hediger, 1955, 1964) and poor diet (Allen & Ullrey, 2004; Crawford, 1968; Oftedal & Allen, 1996).

As well as the rate at which offspring are produced, the sex of those offspring is an important factor that mothers can adaptively manipulate (Charnov, 1982; Hardy, 2002; Trivers & Willard, 1973). Sex allocation theory predicts that, in sexually dimorphic species in which males are more costly to produce, mothers in good condition should bias their offspring sex ratio in favour of males because it is the sex that generally yields the highest marginal fitness returns (Clutton-Brock *et al.*, 1982; Sieff, 1990), an idea supported by various empirical studies (Cameron &

Linklater, 2000; Clutton-Brock *et al.*, 1986; Monard *et al.*, 1997; Saltz & Rubenstein, 1995; Wilkinson & van Aarde, 2001).

The past four or five decades have witnessed an accumulation of basic descriptions of life-history strategies for an increasing number of terrestrial mammals. A few of these studies have explicitly assessed within-species differences in life history strategies by comparing demographic performance between social groups or keeping systems, such as wild versus captive-born (Bryant, 2005; Snyder *et al.*, 1996; Swaisgood *et al.*, 2006; Woodley *et al.*, 1997), farm versus zoo populations (Asher et al., 1999; Thévenon et al., 2003) or zoo versus native populations (Courtenay & Santow, 1989; Kurt, 1995; Kurt & Mar, 1996; Laikre, 1999; Taylor & Poole, 1998; Thévenon *et al.*, 2003). For elephants in particular, a few reports have been published on the differences in survival and reproductive patterns of captive elephants between zoo populations and those in the range states (Kurt, 1995; Kurt & Mar, 1996; Schmid, 1998b; Taylor & Poole, 1998).

However, in neither Asian nor African elephants have there yet been direct comparisons of reproductive strategies between captive-born and wild-caught individuals. It is worthwhile conducting such comparisons because most elephants kept in captivity, such as those in zoos, tourist camps or logging camps, are originally derived from wild-caught animals, and any differences between these groups might have important implications for the management of captive populations. In this chapter, I present analyses of the reproductive rates and birth sex ratios of captive-born and wild-caught Asian elephants (*Elephas maximus*) kept for logging in Myanmar. In doing so, I focus on the following key questions:

1. How is female reproductive potential impacted by birth origin (wild-caught versus captive-born)? In this context, I focus on the following indicators of reproductive performance: (a) age-specific fecundity, (b) age at first breeding, and (c) interbirth intervals.

2. Do captive-born or wild-caught elephant females adapt offspring sex ratio in relation to either maternal age or parity?

4.2. Materials and methods

4.2.1. Study population

This study is based on a subset of records from the timber elephant studbook of Myanmar Timber Enterprise, involving females (n = 2841, wild-caught = 1298, captive-born = 1543) with full survival histories (i.e., known ages at entry and departure from the population) and complete calving information. Elephants captured before 1950 are excluded because capture dates were recorded only to the nearest decade (see Chapter 3 Methods for details). The total number of calves in this study is 2044, 63 (3%) of which were stillborn.

Age-specific fecundity (m_x) is the average number of female offspring produced by an individual female between the ages of x and x+1, the number of female live births (b_x) divided by the approximate mid-year population of mothers M in the age class

$$m_x = \frac{2b_x}{M_x + M_{x+1}}$$

The total numbers of female calves born alive from captive-born and wild-caught mothers were 526 and 499 respectively. The youngest age at which a female gave birth was reported as just over five, while previous studies have reported births to mothers as young as seven (Kurt, 1995; Sukumar, 2003a). However, such early births are extremely rare, with only six births (0.3% of total calves) from mothers younger than ten in my data. Wild-caught females captured at less than ten years of age are included in the analyses, assuming they are not likely to reproduce prior to capture. Those wild-caught females captured over ten (n=818) are excluded from analyses because it is impossible to trace the past breeding history before capture.

I also present the seasonal pattern of births. Myanmar has three main seasons, hot season, rainy season and cold season. The hot season (summer) is from March to May, the rainy season (monsoon) is from June to October and the cold season is from November to February.

I conduct a binomial generalized linear model (GLM) using R-software (R version 2.2.1) to test potential determinants of birth sex ratio. A full model containing all explanatory variables and first-order interaction terms was initially fitted. I then carried out model simplification with standard methodology through stepwise deletion (Crawley, 2003; Dalgaard, 2002). Significance was evaluated at the 5% error level using the likelihood ratio chi-square test.

Cox regression analysis was used to test the effects of explanatory variables on age-specific fecundity rate, primiparous age and interbirth interval using R-software (R version 2.2.1). In the case of fecundity rate, mothers' ages at calving, entry to and departure from the population were analysed with histories split at calving (the event of interest), and censoring at population departure (either death or loss to follow up). In the case of interbirth interval, time to event is measured by the difference in the age of mother between two consecutive live births of calves.

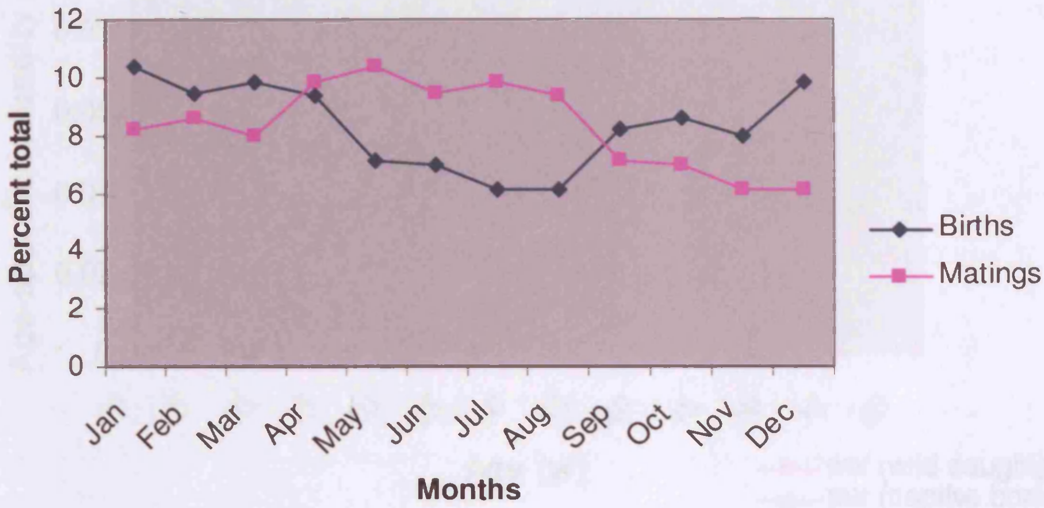
4.3. Results

The youngest and oldest captive-born and wild-caught mothers in this filtered data were recorded as 5.3 and 53 (median = 24.7) and 6.4 and 60.8 (median = 29.3), respectively. The maximum number of calves that a single mother gave birth to in her lifetime was ten.

4.3.1. Seasonality of births and calving rate

Although births are recorded in each month of the year, a lower rate is found in the late summer month of May and early monsoon months from June to August (Figure 4.1). Taking account of the mean gestation period of Myanmar elephants as 20-21 months (Anghi, 1962; Flower, 1943; Hundley, 1922), the peak of mating and conception is likely to be in late summer and the early monsoon.

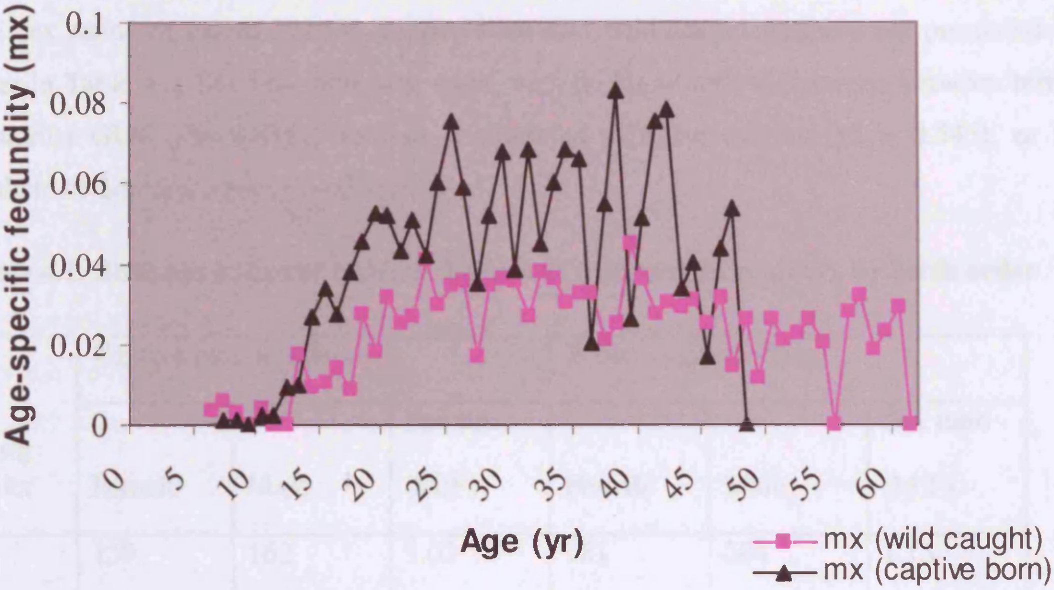
Figure 4.1. Births compared with inferred matings by month. The timing of matings is estimated by subtracting 20.5 months from the dates of birth.



4.3.2. Age-specific fecundity rate

Cox regression analysis showed that the fecundity of captive-born mothers is significantly higher than that of wild-caught mothers (Figure 4.2, Cox regression test statistic, $Z = 11.9$, $P < 0.001$), with rates proportional across ages (Cox proportional hazards test statistic $\chi2 = 0.37$, $P = 0.54$). In both groups, fecundity peaks between the ages of 25 and 40. Over this period, fecundity is about 70% higher in captive born than in wild caught mothers (0.053 versus 0.032 live female calves per mother per year on average). After 40, there is slight reproductive senescence, with complete cessation of breeding at the ages of 49 and 61 in captive born and wild caught mothers respectively. However, this apparent cessation is not a robust result, since there are very few potential mothers surviving beyond these ages (25 and 31 captive born and wild caught mothers respectively, with no captive born mothers by the age of 54). Adding to this the fact that, in wild caught mothers, fecundity remains relatively high at around 0.02 into their early 50's, there is no evidence for a clear age at which reproduction ceases in either group.

Figure 4.2. Age-specific fecundity rates of captive-born and wild-caught mothers



4.3.3. Age at first breeding

The earliest onset of breeding occurred at about the same time in mothers of different birth origins (Figure 4.2). However, primiparous captive-born mothers were significantly younger than their wild-caught counterparts (median ages 21 versus 24, Cox regression test statistic Z = 6.7, P < 0.001, proportionality of hazards test statistic $\chi 2$ = 0.34, P= 0.56).

4.3.4. Interbirth interval

Interbirth interval was analyzed on the basis of 2044 calvings, involving 862 females. The shortest interbirth intervals recorded were 1.52 years for captive-born mothers and 1.71 years for wild-caught mothers. On average, interbirth intervals were significantly shorter in captive born mothers (median= 4.93 years) than wild-caught mothers (median = 5.28 years) (Cox regression test statistic, Z = 5.4, P < 0.001, proportionality of hazards test statistic $\chi 2$ = 0.3, P= 0.58). However, neither sex, birth order, nor birth status (live/stillborn) of the calf significantly influenced interbirth interval, nor were there any significant interactions between any of the explanatory variables investigated.

4.3.5. Birth sex ratio

The sex ratios of calves born to captive-born and wild-caught mothers are presented by birth order in Table 4.1. Sex ratio was near even, with no significant differences between birth orders (binomial GLM $\chi 2= 0.418$), between mothers of different origins ($\chi 2 = 0.545$), or between mothers of different ages ($\chi 2 = 0.785$).

Table 4.1. Birth sex ratios of captive- born and wild-caught mothers by birth order

	Captive born mothers			Wild caught mothers		
Birth order	Female	Male	Sex ratio (M:F)	Female	Male	Sex ratio (M:F)
1	159	162	1.02	181	204	1.13
2	129	136	1.05	125	136	1.09
3	96	87	0.91	79	63	0.80
4	55	59	1.07	37	34	0.92
5	30	33	1.10	17	18	1.06
6	16	15	0.94	12	8	0.67
7	9	8	0.89	0	5	-
8	3	5	1.67	0	0	-
9	1	2	2.00	0	0	-
10	0	2	-	0	0	-
Total	498	509	1.02	451	468	1.04

4.4. Discussion

4.4.1. Seasonality of births

Brown and Shine (2006) commented that seasonal reproduction can happen in tropical animals, similar to temperate-zone animals, giving distinct seasonal peaks in reproductive activity. In some cases, reproductive activity is spread out over weeks or months, but nonetheless is clearly seasonal rather than continuous (Aung et al., 2001; Bronson, 1995; Bronson & Heideman, 1994). Even *Homo sapiens*, the archetypal example of a continuously breeding species, exhibits significant seasonality in births (Bronson, 1995; Bronson & Heideman, 1994). Studies have shown that seasonal reproduction can be initiated by day length (Daunt et al., 2006; Helm & Gwinner, 2005), temperature (Perfito et al., 2005), rainfall (Gaillard *et al.*, 1993; Patterson, 1991), food supply (Fanjul et al., 2006; Forcada & Abecia, 2006) or interactions between these factors (Gaillard et al., 1993; Perfito et al., 2005; Toigo et al., 2006)

The pattern of reproductive output of timber elephants is not strongly seasonal, but shows a slight peak in the cool moths of December and January. This is consistent with the findings of Toke Gale (1971), and is likely to be driven by the seasonal availability of good quality forage. There is generally less good forage available in the hot summer and humid early monsoon period, but better conditions towards the end of the monsoon and into the cool months that follow. Similar seasonal adaptation of elephant calving patterns to feeding conditions was reported by Sukumar (2003), who reported that births are distributed towards the end of wet season and before the arrival of monsoon in south India. Likewise, a clear seasonality of conceptions corresponding to rainfall has been reported in African elephants (Hanks, 1969).

Based on a mean gestation period for Myanmar elephants of 20-21 months (Anghi, 1962; Flower, 1943; Hundley, 1922), peak mating and conception coincides with the summer rest period. According to the studies of reproductive seasonality in *Cervis eldi thamin*, a polygynous endemic tropical deer in central Myanmar (Aung et al., 2001), reproduction is also seasonal, with mating occurring during the hot-dry season and parturition in the cool months of November-December (Monfort et al., 1990). Elephants in my study show a similar breeding pattern. High conception in the summer rest period coincides with a high incidence of musth among bulls according to U Toke Gale (1971), as well as with round-the-clock foraging and more time for socialization than in the work season.

4.4.2. Age-specific fecundity rate

Wild-caught and captive-born mothers showed similar fecundity patterns, with maximal rates in adults aged between 25 and 40. However, the maximum fecundity of captive-born mothers was 70% higher than that of wild-born mothers. This may be due to a reduced availability of food, capture/training stress or a combination of the two. Food deprivation or restricted food intake can suppress ovulation, estrus behavior and mothering ability in various mammals (Borwick *et al.*, 1997; Robinson *et al.*, 2006; Wade & Schneider, 1992) including humans (Lummaa & Tremblay, 2003). Although no study has been conducted on the feeding ecology of captive elephants, it is expected that captive-born and wild-caught elephants may differ in their abilities to extract high quality resources from their foraging environment. Having been born in the area in which they live and forage, captive-born elephants are more likely to have knowledge of high quality resources. Wild-caught elephants are also more likely to experience lower nutrition in the early post-capture period due to the unfamiliarity with good foraging areas. In addition, they may have difficulty competing with resident captive-born elephants for the best forage sites. This may be partly due to a restricted ability to move because their front feet are fettered when they are released into the forest at night to forage.

Wild-caught elephants also are more likely to suffer from stress than captive-born animals, for two possible reasons. First, in elephants captured young, early life experience can have a lasting effect in adulthood. For example, research has shown that maternal separation and early life environmental stress predisposed to various pathologies in later life (Lummaa & Clutton-Brock, 2002a; Shanks, 2002), including a permanent effect on reproductive success (Albon et al., 1987). Second, taming/breaking follows immediately after capture and is generally more traumatic for wild caught than for captive born animals. For elephants captured at breeding age, the direct psychological and physical trauma sustained during the early days in captivity could therefore also play a part in depressing the fecundity of wild caught elephants. I explore this question in more detail in Chapter 5.

4.4.3. Age at first birth

Age of first reproduction can affect individual fitness (Bell, 1980) and population dynamics (Festa-Bianchet *et al.*, 1995; Reiter & Leboeuf, 1991). Among ungulates (Saether et al., 1996) and primates (Parga & Lessnau, 2005), body size and body condition are reported to affect age at maturity; early-maturing females are often larger than late-maturing females (Gaillard et al., 1992), because females with retarded growth or low body mass require more years to attain adult body mass before they start reproducing (Langvatn et al., 1996). As in the observed difference in fecundity between captive-born and wild-caught mothers (see 4.4.2), capture and taming-related stress with additional effects of malnutrition may be responsible for the delayed attainment of reproductive maturity in wild-caught female elephants.

4.4.4. Interbirth interval

The average gestation period in Asian elephants is just over 21 months (Schmidt, 2006), and allowing for a delay to re-conception, the minimum intercalving interval is therefore often assumed to be around 2 years (Gee, 1955; Sukumar, 2003b; Yin, 1962). The results of this study indicate a minimum inter-birth interval of a little over 18 months, indicating that gestation length can be can be considerably shorter than the often-quoted average. While this result seems exceptional in the context of most recent literature, it is consistent with earlier literature reporting a minimum gestation period of 17 months 17 days (1.46 years) (Burne, 1943). Nonetheless, it is possible that this extremely short interval is the result of a recording or transcription error, highlighting the need for accurate data recording and checking in future.

Numerous physiological and behavioral mechanisms link reproduction and energy metabolism. A complete reproductive cycle of ovulation, conception, pregnancy, lactation and offspring care is one of the most energetically expensive activities that a female mammal can undertake. We therefore expect that nutritional constraints should suppress breeding, and hence lead to longer interbirth intervals. For example, in other large mammals such as African elephants, *Loxodonta africana* (Laws & Parker, 1968; Laws et al., 1975) and white rhinoceros, *Ceratotherium simum* (Rachlow & Berger, 1998), females in high-density populations experience more intense competition for food, and exhibit longer intervals between births than those in lower-density areas. Lactation is by far the most energy demanding phase of reproduction for female mammals (Gittleman & Thompson, 1988; Millar, 1979; Oftedal, 1984). In this study, I expected male calves to be more demanding of mothers during lactation, and hence to be associated with extended inter-birth intervals, but this was not found to be the case. This suggests that any additional costs of male calves are relatively small and easily compensated for in this population. Similar results are reported by (Green & Rothstein, 1991a; Le Boeuf & Reiter, 1988) suggesting that offspring sex did not affect interbirth intervals and probability of mothers' survival or fecundity in sexually dimorphic mammals. I also expected first-born calves to show longer subsequent birth intervals, because primiparous mothers were likely to be younger and less well grown. Similar examples come from primate studies, indicating primiparous females tended to have longer interbirth interval (Koyama et al., 1992; Smuts & Nicolson, 1989). Again, this expectation was not supported, suggesting that females do not generally conceive before they are physiologically well able to support pregnancy and lactation. Finally, the origin of the mother did have a significant effect, with longer inter-birth intervals in wild-caught mothers. This is likely to be due to a combination of reduced nutrition and increased stress in wild-caught mothers in the post-capture period (see Section 4.4.2 above).

4.4.5. Birth sex ratio

Sex allocation theory suggests that sex ratio at birth should be affected by multiple influences, particularly resource availability (Gosling, 1986). According to Sheldon and West (2004), in polygynous ungulate mammals, there was a weak but significant correlation between maternal condition and sex ratio. They also claimed that such a relationship was stronger when sexual size dimorphism was more male biased and when gestation periods are longer. As the more costly sex, mothers are expected to invest in males only when their body condition or nutritional options are good, and good conditions are therefore expected to lead to a male biased sex ratio (Kojola, 1997; Rivers & Crawford, 1974); Kohlmann 1999).

In this study, captive born mothers are expected to be in better condition because they are less stressed and suffer less from competition for food. Similarly, I expect multiparous mothers to be older, larger and on average in better condition than primiparous mothers. However, the resulting predictions of male-biased birth sex ratio in these groups are not supported by the data, which show no significant deviation from even birth sex ratio in any group. While this result does not support sex allocation theory, it is consistent with findings in another captive Indian elephant population (Sukumar, 2003b), and in some other large land mammals such as African elephant (Lee & Moss, 1986; Moss, 2001) and captive giraffes (Bercovitch et al., 2004).

4.5. Conclusion

Large mammal populations are characterized by long life-expectancies, delayed sexual maturity and low reproductive rates (Harvey & Zammuto, 1985). In this study, I present the seasonal calving pattern of logging female elephants, which prefer to give birth in the cooler months and during the late monsoon season. My results indicated that different maternal birth origins show different fecundity rates, with captive-born mothers having significantly higher rates than wild-caught mothers. This is likely due to an extended downstream effect on fitness, resulting from harsh capture and breaking procedures on wild caught females. It is also likely that inadequate nutrition contributes to the low reproductive rates in wild-caught females. This finding was strengthened by further analyses of the effects of birth order, sex of calves and birth origins of mothers on the interbirth interval, where I found that wild-caught mothers exhibit a significantly lower birth rate than captive-born mothers by prolonging the interbirth interval. Fecundity peaks between 25 and 40 years of age in both wild-caught and captive-born females, then gradually declines, although there is no clear evidence of complete reproductive cessation. Inter-birth intervals were significantly longer in captive born than wild-caught mothers. In sum, the evidence suggests that fecundity is greatest among captive-born females. Given this, and the negative consequences of capturing and training wild-born females, the most humane and efficient way to sustain working populations of Asian elephants should be through well-planned improvements to captive breeding efforts.

Chapter 5. The effects of captivity on the survival and fecundity of captive timber elephants

5.1. Introduction

Life-history theory has experienced dramatic growth and elaboration in anthropology in the past decades (Hill & Kaplan, 1999). It identifies two conceptual distinct efforts, known as somatic and reproductive efforts that are critical to an individual's biological success (Hirshfield & Tinkle, 1975; MacDonald & Hewlett, 1999). Somatic effort refers to individual's physical survival while reproductive effort attempts to copy one's self into subsequent generations and this effort can sub-divide into three categories such as mating effort, parenting effort and nepotistic effort (Hirshfield & Tinkle, 1975; MacDonald & Hewlett, 1999).

Parental attributes are generally considered maternal effects, where a parent's phenotype or environment affect the expression of phenotypic characters in the offspring (Mousseau & Fox, 1998a; Mousseau & Fox, 1998b). The term 'maternal effects' is generally used because of the predominance of the mother's nongenetic effects on offspring phenotype (Bernardo, 1996; Mousseau & Fox, 1998a; Rossiter, 1991). Several theoretical studies have illustrated the potential role of maternal effects in the evolution of polygenic traits (Kirkpatrick *et al.*, 1989; Rossiter, 1991). Maternal effects can accelerate or dampen the rate of evolution of characters, change the direction of evolution, and even induce maladaptive responses to selection (Bernardo, 1996; Kirkpatrick *et al.*, 1989; Wolff, 1988)

To date, most studies have documented that maternal fitness and her social environment are key features influencing life-history strategies (Altmann & Alberts, 2005; Johnson, 2003b; Jokela, 1998). This study will present how non-heritable, maternally-mediated effects influence the survival and reproductive potential of the next generation in captive Asian elephants.

When animals are captured for various reasons, captivity can affect the survival and reproductive efforts of captured animals at a range of temporal scales (Bryant, 2005; Williamsblangero *et al.*, 1992). Most immediately, the direct impact of capture is likely to reduce demographic rates in the short term through environmentally-mediated effects. For example, severe stress due to capture procedures has been shown to cause reduced food intake, leading to growth retardation in rodents (Santos et al., 2000), and reduced immunocompetence in primates (Suleman et al., 2004; Suleman et al., 1999). Both of these factors are likely to reduce rates of survival and fecundity. In the case of Asian elephants, training involves the process of "breaking", a highly stressful procedure that takes place immediately after capture. Evidence presented in Chapters 3 and 4 suggested that survival and fecundity are both depressed by capture and breaking.

Over time, captured animals may adapt to the captive environment (Mignon-Grasteau *et al.*, 2005; Price, 1984). Such adaptation to captivity by individuals during their lifetime requires the development of coping responses to chronic stressors (Cooper & Albentosa, 2005), a process that can be assisted by appropriate environmental conditions (Lickliter & Ness, 1990) and husbandry techniques (Price, 1984; Price, 1999). However, full adaptation to captivity is not always assured. For example, studies in animals (Clutton-Brock *et al.*, 1987b; Fox & Mousseau, 1998; Taborsky, 2006) and humans (Lummaa & Clutton-Brock, 2002a) show that adverse conditions in early life (such as limited nutrition, stress or inadequate maternal care) can programme the activity of the hypothalamic-pituitary-adrenal axis, leading to metabolic and psychiatric disorders and depressed immune responses later in life (Shanks, 2002; Veenema *et al.*, 2006). Early capture stress may therefore lead to lasting depression of demographic rates throughout the animal's life-span.

In the medium term, captivity may influence the demography of later generations through non-genetic maternal effects. For example, in humans, adverse environmental influences can exert downstream effects on the growth and subsequent reproductive success of their offspring (Lummaa & Clutton-Brock, 2002a). Similarly in birds, poorer maternal state prior to breeding can give rise to offspring with lower fecundity than offspring from birds in a better nutritional state (Gorman & Nager, 2004). Compelling evidence is now available that such developmental responses may last several generations in animals (Huck *et al.*, 1987; Marchlewska-Koj, 1997) and humans (Lumey & Stein, 1997).

Finally, in the long term, selection can lead to genetic changes in the captive population, ultimately giving rise to domestication. For example, a long-term experiment on fox domestication (Belyaev *et al.*, 1984; Belyaev & Trut, 1975) has shown that, after 18 generations of selection, captive silver foxes (*Vulpes fulvus*), had reduced cortisol levels and reduced fear when faced with humans, and that this trait of tameness is genetically controlled.

When large animals, such as camel, buffalo or elephant, are used for draught purposes, human and animal share the same work space without any barrier between them, and human dominance over the animal is therefore a necessity (Fernando, 1898; Koehl, 2000). However, the effects of capture and captivity on survival and reproductive patterns under these circumstances are largely unknown (Tenhumberg *et al.*, 2004). This is particularly true of intergenerational effects, which have not previously been explored in long-lived, large-bodied animals. In this chapter, I explore whether capture and captivity can cause changes in the survival and reproductive rates of the captive elephants of Myanmar at three temporal scales: 1) short-term capture effects on individuals, 2) long-term capture effects on individuals, and 3) differences between generations mediated by maternal effects. While there are likely to be long-term intergenerational effects, mediated by selection and genetic change, the data available cannot address this temporal scale. I therefore focus on the following specific questions:

1. Are there any changes in survivorship, age at first reproduction or fecundity between individuals with different lengths of ancestral history in captivity?

2. Can lower survivorship and fecundity in wild caught elephants (Chapters 3 and 4) be explained by a temporary effect of capture?

3. Do residual difference in survivorship and fecundity persist after controlling for any temporary capture effects?

5.2. Materials and methods

Among the 5213 elephants with complete life history biodata (see Chapter 2 for details), 39.8% (n=2076) are wild-caught elephants and they are coded as G1 (first generation) elephants. Direct descendents of these elephants (n=1549) are coded as G2 (second generation) and those born in the next generation (the grand-offspring of wild-caught mothers, n=1052) are coded as G3 (third generation) elephants. Some captive-born elephants (n=536) have missing maternal information and they are excluded from the analysis of intergenerational difference in survival, leaving 4677 elephants among which to explore effects on survival. Fecundity effects are explored among 998 females, which gave birth to a total of 1328 calves. For intergeneration difference in primiparous age, wild-caught (G1) females (n=1042) with estimated capture age over 10 year are excluded, because their reproductive history before capture is impossible to obtain. The birthing records of 877 calves and fecundity history of 1757 females are used in exploring the intergenerational differences in primiparous age.

The Cox proportional hazard model is used to test the effects of time in captivity on demographic rates. This is the most general of the survival analysis models because it is not based on any assumptions concerning the nature or shape of the underlying survival distribution. Survival analysis models the time to a given event, in this case "death" for survival analysis, and "birth" for the analyses of fecundity and age at first reproduction. To look for temporary, short-term effects of capture on demographic rates, survival analysis is conducted with time since capture as a time-dependent explanatory variable (Anderson & Gill, 1982). This is achieved by cutting the histories of individual wild-caught elephants into annual increments following capture, and analyzing survival or fecundity with year since capture as an explanatory variable. Hazard plotting is based on the concept of the hazard function of a distribution (Nelson, 2000). The hazard function is so called the instantaneous failure rate and force of mortality. The cumulative hazard function, $H(x)$, of a distribution is the integral of the hazard function up to time (x) (Nelson, 2000) or the instantaneous potential for failing at time (x) per unit time, given survival up to time x (Kleinbaum, 1996). Free statistical software package 'R' (version 1.9.0, released 2004-04-12, web address: http://cran.r-project.org/) and SPSS (Statistical Package for the Social Services, version 15, released 2007, SPSS Inc.,Chicago, Illinois) are used for survival analysis.

5.3. Results

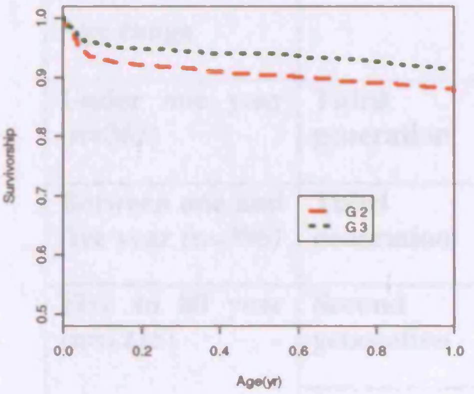
5.3.1. Intergenerational difference in survival

As there were very few elephants captured before the age of five, intergenerational differences in survival below this age were compared only between second and the third generations in captivity. Second generation calves (aged 0-5) had higher mortality than the third generation, but the comparison had significant non-proportionality in the hazard function (Cox proportional hazards test χ 2 = 0.067, P = 0.04). The data are therefore split into shorter age ranges, under-one year and those aged between one and five, in which the underlying hazard functions are proportional. In both under-one and between one and five age groups, Cox regression analysis indicates that the third generation elephants have significantly higher survival rate than the second generation calves (Table 5.1 and Figure 5.1a and b).

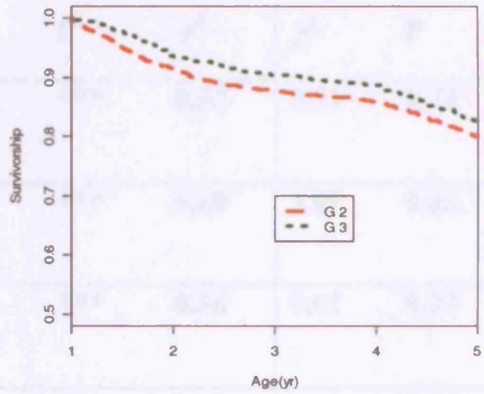
For elephants aged over five, there are clear differences in survivorship between generations (Table 5.1 and Figure 5.1c). Among the three generations, the first-generation elephants show the lowest survival rate; mortality rates of second and third generation elephants were respectively 44 and 38 percent lower than in first generation animals, and hazard functions were proportional in both generations. Comparing within captive-born elephants, the third-generation shows an 11% higher mortality rate than the second-generation, however, this difference is not significant (ANOVA, test statistics= 0.81, P=0.37).

Figure 5.1. Survivorship curves of timber elephants by generations in captivity (G1= the first generation elephants, i.e. wild caught, G2 = second generation elephants and G3= third generation elephants).

a) Under one year



b) Aged between one and five years



c) Over-five year

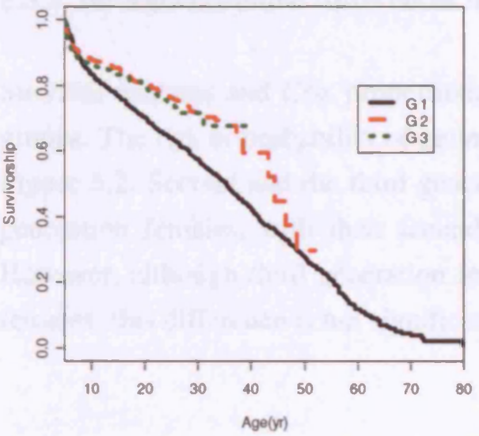


Table 5.1. Cox regression model results for age-specific survival rates by generations in captivity and by age groups. The baseline categories are G2 (second generation in captivity) for calves (under 5), G1 (first generation in captivity) for the 5+ age group. (Z = text statistics, P = probability, e^{β} =exponential coefficient, level of significance ***= P<0.001).

Age range	Generations	Cox regression			Proportionality	
		Z	P	e^{β}	χ^2	P
Under one year (n=363)	**Third generation**	**-4.68**	***	**0.52**	**0.71**	**0.40**
Between one and five year (n=396)	**Third generation**	**-3.28**	***	**0.69**	**3.07**	**0.08**
Five to 80 year (n=1215)	**Second generation**	**-6.56**	***	**0.56**	**0.01**	**0.94**
	Third generation	**-4.43**	***	**0.62**	**0.21**	**0.64**

5.3.2. Intergenerational differences in fecundity

Survival analysis and Cox proportional hazard models are used to compare fecundity between groups. The risk or probability of giving birth in captivity is compared by mothers' generations in Figure 5.2. Second and the third generation females are significantly more productive than first generation females, with their fecundity rates respectively 27% and 55% higher (Table 5.2). However, although third generation females have 22% higher fecundity than second generation females, this difference is not significant (ANOVA test statistics 2.94, P=0.09).

Figure 5.2. Cummulative probability of giving birth is compared by generation, with adjustment for maternal age (G1= first generation, G2= second generation and G3= third generation).

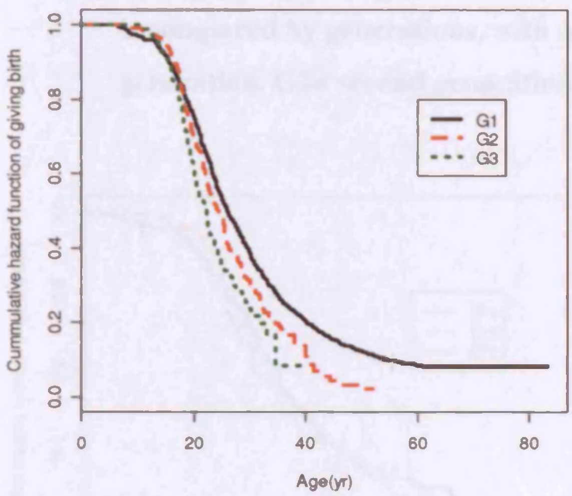


Table 5.2. Cox regression model results of fecundity by generations. The baseline category is G1 (first generation in captivity). (Z = text statistics, P = probability, e^{β} = exponential coefficient, level of significance *** = P<0.001).

Generations	Cox regression			Proportionality	
	Z	*P*	e^{β}	χ^2	*P*
The second generation	**3.05**	***	**1.27**	**1.25**	**0.26**
The third generation	**4.26**	***	**1.55**	**0.02**	**0.88**

5.3.3. Intergenerational differences in age at first reproduction

For the analysis of intergenerational differences in primiparous age, females captured below the age of 10 are used. The median age at first reproduction is almost identical between first and second generation females, slightly lower in third generation females (respectively 24.8 yr, 25.3 yr and 22.8 yr in first, second and third generation females). However, Cox regression analysis reveals that these differences are not significantly different (Table 5.3). When the primiparous ages of second and third generation mothers are compared, this difference is not significantly different (ANOVA test statistics 0.61, P = 0.43). The graphical appearance of the cumulative risk of giving birth by primiparous mothers by generations is presented in Figure 5.3.

Figure 5.3. Cummulative hazard function of giving birth by primiparous mothers is compared by generations, with adjustment for maternal age (G1= first generation, G2= second generation and G3= third generation).

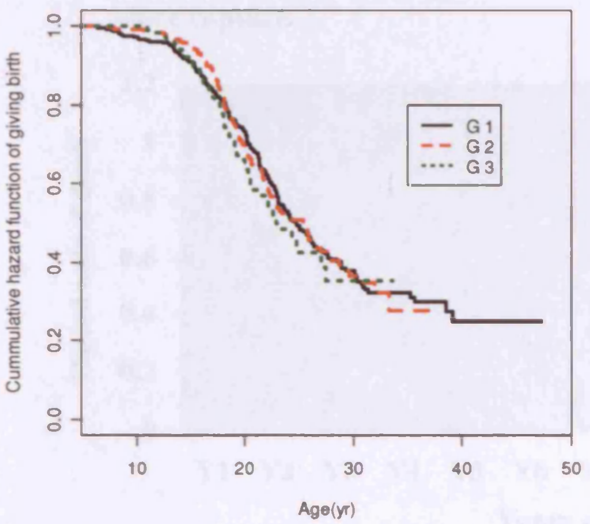


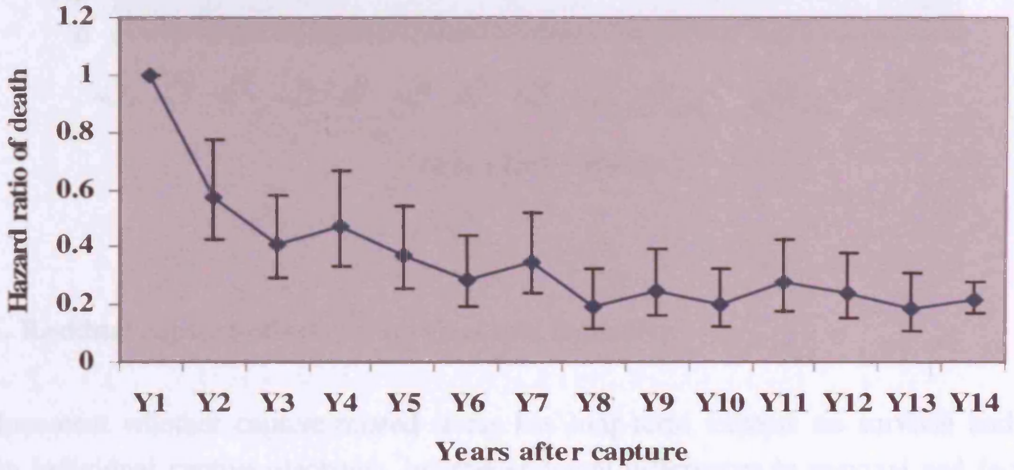
Table 5.3. Cox regression model results for maternal age at firth birth in captivity by generations. The baseline category is G1 (first generation in captivity). (Z = text statistics, P = probability, e^{β} = exponential coefficient).

Generations	Cox regression			Proportionality	
	Z	*P*	e^{β}	χ^2	*P*
The second generation	**-0.11**	**0.91**	**0.99**	**1.27**	**0.26**
The third generation	**0.77**	**0.44**	**1.12**	**0.01**	**0.92**

5.3.4. Short-term effect of capture and breaking in wild-caught elephants

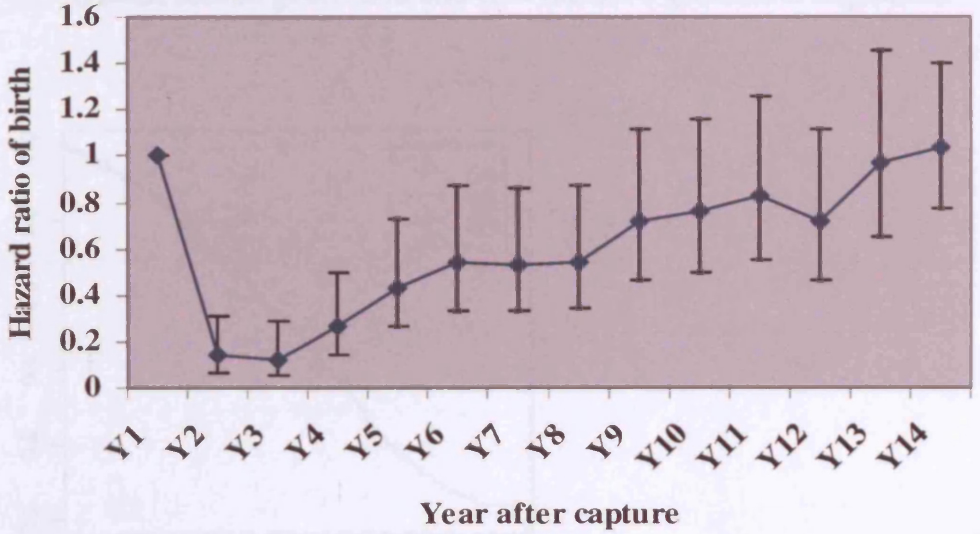
Figure 5.4 shows the pattern of relative mortality rates over a period of 14 years after capture. The highest mortality is in the first year after capture, with a rapid improvement over the next two years. However, a gradual reduction in mortality rate can be detected up to the eighth year after capture, with low and stable mortality thereafter, suggesting that it takes up to eight years to recover fully from direct capture-related stress in wild-caught elephants.

Figure 5.4. Survival rate hazard ratios (with 95% confidence limits) over time since capture.



Using the same approach as in the above analysis of survival rates, I investigated whether there was a temporary capture effect on fecundity (Figure 5.5). Fecundity in the first year after capture reflects mothers already pregnant when captured, so provides a baseline "natural" fecundity rate against which to compare subsequent changes. The lowest fecundity rate was in the second year after capture, after which fecundity gradually increased over time. Fecundity rate remained lower than that in the first year after capture until the 13th year, although the difference was not statistically significant by the fifth year.

Figure 5.5. Fecundity rate hazard ratios (with 95% confidence limits) over time since capture.



5.3.5. Residual capture effects on survival and fecundity

To document whether capture-related stress has long-term impacts on survival and fecundity within individual captive elephants, intergenerational differences in survival and fecundity are tested again after controlling for the temporary capture effects shown above. This was done by removing the first seven years after capture from the histories of G1 elephants' in the case of survival analysis, and the first 12 years in the case of fecundity analysis. I find that, although the mortality rate remained slightly higher in wild-caught elephants, there were no longer any significant differences in mortality rates between elephants of the three generations (Figure 5.6, Table 5.4). Similarly in the case of fecundity, after controlling for the temporary capture effect, there were no significant difference in fecundity between elephants of the three generations (Table 5.5).

Figure 5.6. Survivorship curves of timber elephants by generations in captivity after controlling for the temporary capture effect (G1= the first generation, G2=the second generation and G3= the third generation elephants).

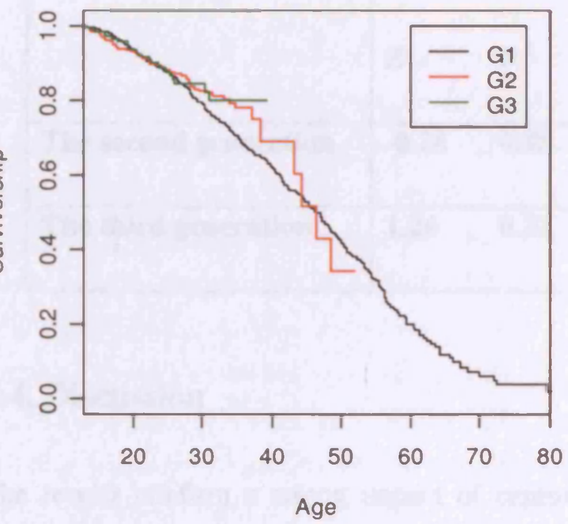


Table 5.4. Cox regression model results for survival by generations in captivity after controlling the temporary capture effect (Z = text statistics, P = probability, e^{β} = exponential coefficient).

Generations	Cox regression			Proportionality	
	Z	*P*	e^{β}	X^2	*P*
The second generation	**1.91**	**0.06**	**0.77**	**0.34**	**0.56**
The third generation	**1.18**	**0.24**	**0.79**	**0.07**	**0.80**

Table 5.5. Cox regression model results for fecundity by generations in captivity after controlling for the temporary capture effect (Z = text statistics, P = probability, e^{β} = exponential coefficient).

Generations	Cox regression			Proportionality	
	Z	*P*	e^{β}	X^2	*P*
The second generation	**-0.28**	**0.98**	**1.00**	**1.22**	**0.27**
The third generation	**1.26**	**0.21**	**1.16**	**0.01**	**0.94**

5.4. Discussion

The results confirm a strong impact of capture stress on newly-caught elephants, and further demonstrate that this impact lasts for several years after capture, perhaps up to 12 years in the case of the fecundity effect. However, having recovered from initial capture effects, there appears to be no lasting effect of capture on individuals. In terms of maternal effects, elephants with mothers who were wild-caught rather than captive-born had significantly higher infant mortality, and a non-significant tendency to lower fecundity later in life. These results suggest that, although individuals are able to shake off the negative impact of capture on demography within their own life-time, the effects reappear in their offspring.

Capture-induced stress is well known to impact on demography (Cabezas et al., 2007; Jessop et al., 2003; Reeder & Kramer, 2005). Multiple pathways of stress initiate the acute stimulation of the sympathetic nervous system and the hypothalamic-pituitary-adrenal axis (Curry, 1999). The physiological and pathological consequences of the activation of these pathways can include depressed immune function (Dohms & Metz, 1991; Matson et al., 2006), reduced survival (Baker et al., 1998; Boivin et al., 2006), suppressed reproduction (Bentley-Condit & Smith, 1997; Lance & Elsey, 1986; Lance et al., 2004; Nepomnaschy et al., 2004; Wingfield & Sapolsky, 2003), and retarded growth rate (Morgan & Tromborg, 2007), and these effects have been recorded in many species (e.g., black rhinoceroses *Diceros bicornis* (Kock et al., 1990), roe deer *Capreolus capreolus* (Calenge et al., 2005), bighorn sheep *Ovis canadensis* (Pistorius et al., 1999), baboons *Papio* spp. (Bentley-Condit & Smith, 1997), and African green monkeys *Cercopithecus aethiops*

(Suleman et al., 2000)). Other long-term studies monitoring mortality rates of captured ungulates have reported that capture-related mortality is detectable up to ten years after capture (Arnemo et al., 2006). On the other hand, studies on some primates (Blank et al., 1983; Walker et al., 1982) and carnivores (Ginsberg et al., 1995) indicate that handling, restraint and confinement have no effect on the longevity of these animals.

The long duration of capture-related depression of survival and fecundity in this study is likely to be caused by chronic stress (Morgan & Tromborg, 2007; Sapolsky, 1994; Wingfield & Sapolsky, 2003). Most elephants are captured at a relatively young age, causing their social structure to collapse with the loss of their mentors at a time when their independent foraging skills are still insufficient to meet their requirements. Furthermore, young elephants still depend on their mothers, allo-mothers and older herd-mates for protection and comfort, and have not yet attained adult body mass. At the same time, the unfamiliarity with the terrain and feeding grounds in captive environments, and limited mobility due to unfamiliarity with the fettering chain which is traditionally attached to all captive elephants during night foraging, could have caused inadequate feeding, leading to retarded growth and decreased immunocompetance in captured elephants. In many animal species, social defeat is a powerful stressor that can lead to drastic alterations in physiology and behaviour, especially if the stressor remains for a long period. Compelling evidence is now available that stressful events inhibit survival in humans (Boivin et al., 2006) and in nonhuman primates (Rowell, 1970; Wasser & Barash, 1983; Wingfield & Sapolsky, 2003). Similarly, separation from herd-mates is likely to be a powerful early adverse experience in elephants (Bradshaw et al., 2005; Veenema et al., 2006).

Reduced survivorship in the calves of wild-caught mothers is likely to result from the same processes that lead to reduced survival and fecundity in the mothers themselves. The results of this study also suggest that there may be a weak long term effect of prenatal and neonatal conditions later in life. This trend is consistent with many studies showing that the early growth and development of an individual profoundly impacts its reproductive success later in life in various animals (Albon *et al.*, 1987; Gustafsson & Sutherland, 1988), and in humans (Lumey & Stein, 1997; Lummaa & Clutton-Brock, 2002a; Lummaa & Clutton-Brock, 2002b). It is thought that wild-caught mothers' poor nutritional status during pregnancy and calf rearing may hinder immunological maturation in infants, leading to depressed demographic rates in the their offspring, which are G2 individuals in my study through a process known as foetal programming (Bateson *et al.*, 2004; Lucas, 1991, 1998). Stressed, poorly nourished first generation (G1) mothers not only suffer direct impacts, but are also less able to bear and raise calves effectively. The likely mechanisms are through inadequate nutrition and psychological and physical trauma during the early years in captivity, which is likely to be worsened by work-related stress. They may have delayed their first birth until fully recovered from such stress.

5.5. Conclusion

Various studies have documented that coping mechanisms depend on the species, age, sex, diet, previous experience of capture, and the manner in which they are maintained in captivity (Blank et al., 1983; Jones et al., 2000; Jones & Widemo, 2005; Meehan & Mench, 2007; Mendl & Deag, 1995; Walker et al., 1982). In this study, I have shown that the stress of capture in first-generation (wild-caught) elephants causes reductions in survival and fecundity, and that these reduction can be detected up to seven (for survival) or 12 (for fecundity) years after capture. Second generation elephants also suffer from reduced survival as calves, but this impact does not last into adulthood. However, there was some evidence that third-generation elephants were better adapted to captivity than their ancestors in terms of higher reproduction and survival. Although the age of mothers at first birth are not significantly different among generations, the average age at first birth of the third-generation mothers tend to be youngest among the three generations, and their fecundity was also slightly higher. The intergeneration differences in mortality and fecundity are likely to be the result of the synergistic effect of maternal downstream effect and capture-related stress of mothers. Thus I have shown that (1) the process of capture followed by taming is costly for Asian elephants, (2) increasing time in captivity can accelerate the development of reproductive capabilities in captive Asian elephants in terms of age at first birth and calving potential, (3) although the negative impact of capture-related stress on fecundity and survival disappeared within the life-time of wild-caught elephants, the effects reappear in their offspring and (4) maternal environmental effects early in life are an important source of variation in offspring fitness, influencing optimal reproductive strategies at later ages.

Chapter 6. General discussion

The major aim of this thesis is to analyze the factors regulating life history strategies of captive timber elephants in Myanmar. Metabolic rate (Harvey *et al.*, 1991), growth rate (McNab, 1986), body size (Purvis, 2001), brain size (Promislow & Harvey, 1991; Ricklefs & Scheuerlein, 2001), environmental stress (Bijlsma & Loeschcke, 2005; Lumey & Stein, 1997) and domestication (Boice, 1973; Fox, 1978; Hindar *et al.*, 2006; Metcalfe *et al.*, 2003; Petersson *et al.*, 1996) are considered to be important factors influencing life history traits in many animals. In this thesis, I focus on the determinants of age-specific mortality and fecundity captive elephants used as draught animals, with particular emphasis on the effects of capture and taming. Furthermore, I discuss several issues related to the long-term effect of capture on life history strategy of captive working elephants. Detailed discussions of the findings for each of the central data chapters are provided within those chapters. Here, I briefly outline the main outcome of the data analyses and I then discuss areas for future researches.

In Chapter 2, I present the basic demographic parameters of Asian elephants (*Elephas maximus*) in captivity. Separate life-table analyses are conducted on captive-born and wild-caught elephant populations and I reported that, while the captive-born sector of the timber elephant population is self-sustaining, the wild-caught sector would not be if the demographic conditions experienced were maintained in the long run.

Chapter 3 investigates the patterns of mortality in elephants, and explores the determinants of these patterns. Survival analysis revealed that the first year survival rate is 90%. Among the under-five age group, male calves and calves born to wild–caught mothers show significantly lower survival rates than their counterparts. Survival analysis of older age groups indicates that wild-caught and male elephants suffered significantly higher mortality than their counterparts. Using data from International Species Information System (ISIS), a recently published article (Kohler *et al.*, 2006) reported that among most mammalian species kept in zoos, female survivorship significantly exceeds that of males above age five, which is consistent with my studies. However, contrary to my results, survival in zoo animals did not differ significantly between wild-born and captive-born animals. This difference is probably largely due to the fact that the ISIS data rarely start from the moment of capture, and that many species will adapt more quickly to captivity than elephants. The risky nature of capture in elephants was highlighted in Chapter 3 by the difference in mortality rates by capture methods, with elephants captured by immobilization showing the lowest survival rate when compared with elephants captured by milarshikar and stockade.

Chapter 4 examines age-specific reproductive rates, offspring sex ratios in captive-born and wild-caught females, and the effects of mothers' birth origin, mother's age, sex and the birth order of calves on interbirth interval. I report that neither captive-born nor wild-caught mothers adapt offspring sex ratio. However, the mothers' birth origin influences the interbirth interval, with longer intervals in wild-caught than in captive-born females, indicating that reproductive fitness is lower in wild-caught elephant females than captive born females.

Prolonged confinement with limited exercise combined with an unnaturally nutritious diet and inappropriate housing and herd structure are blamed for the poor fecundity and high mortality of zoo elephants in the Western hemisphere (Clubb & Mason, 2002; Hildebrandt *et al.*, 2006; Taylor & Poole, 1998) but no previously published work exists on effect of capture on life history strategies of captive elephants. In Chapter 5, I show that the direct negative effects of capture on elephants last up to 12 years after the capture event, and that the calves of wild-caught mothers also show reduced survival early in life, as well as a tendency to lower fecundity as adults, long after the direct effects of capture stress are operating.

6.1. The immediate needs for long-term sustainability of timber elephants in Myanmar

Environmental stress can be characterized as a force shaping adaptation and evolution in changing environments (Bijlsma & Loeschcke, 2005). Extrinsic stress that results from extreme temperature, climatic factors, chemical components and pollution, either naturally occurring or man-made, are regarded as important factors that influence the evolutionary process. For working elephants in this study, capture-, taming- and work-related stresses acted as extrinsic stressors. Similarly, psychogenic factors (stress, anxiety, depression, or other emotional disturbances), exercise, or energy imbalance are reported as factors that decrease longevity and fecundity in humans (Wischmann, 2006) and primates (Kaplan & Manuck, 2004). In this study, I have shown that wild-caught elephants have lower fecundity and survival when compared with captive-born elephants, indicating that extrinsic stress and psychogenic stress can act both independently and synergistically.

The captive-born sector of the timber elephant population is expected to be self-sustaining in the long term, but only just. This leaves little margin for error, and short term trends may well be less favourable, particularly given that poorly performing wild-caught elephants still form a substantial portion of the population. Maintaining a healthy working elephant population is crucial to the conservation of the wild elephant population because if the population does not produce enough recruits to satisfy demand, capture of wild elephants may re-commence, causing substantial impacts on the wild population. Measures to maintain and enhance the sustainability of the captive population are therefore needed, including improved health care, which would have the added benefit of reducing the risk of disease transmission to wild elephants (Deem *et al.*, 2005).

In long-lived large bodied animals with "slow" life histories, such as elephants, population growth rate is very sensitive to changes in survival rates, and relatively insensitive to changes in reproductive parameters (Oli, 2004). In order to implement a self-sustaining population, without relying on recruitment from the wild, a key management goal of Myanma Timber Enterprise might therefore be to improve survival rates in the captive elephant population. However, survival rates in adults are already very high, and there is probably little scope for improving these. Two key age groups where survival rates are lower, and where there may therefore be room for improvement, are neonates and juveniles at weaning/training age (around four to five).

The causes of elevated mortality in juveniles are not certain, however it is likely that risks associated with either the digestive transition during weaning, or training, or both are to blame. The former would indicate management to ensure adequate nutrition at this vulnerable life stage, while the latter would indicate minimising the degree of physical and psychological stress during training. Further work is needed to clarify which approach, if either, is likely to be most feasible and effective.

Improving the survivorship of neonates would require management to minimize stress and optimize nutrition in pregnant and nursing mothers. These measures would be likely to have the added effect of increasing the fecundity of females in captivity, and these two demographic improvements together could substantially increase the growth potential of the population. I discuss the ways in which this might be achieved in the final section, below.

However, some studies have shown that early reproduction can reduce survival and subsequent fecundity (Reiter & Leboeuf, 1991), with higher offspring mortality and longer interbirth interval (Robbins *et al.*, 2006) and such life-history trade-offs within individual might make it difficult to improve one demographic parameter without negatively affecting another. Alternatively, other studies have suggested that females that breed early have better survival and reproductive success than females that first breed at a later age (Clark *et al.*, 1986; Green & Rothstein, 1991b; Lunn *et al.*, 1994; Pistorius *et al.*, 2004), suggesting that individual quality is the main driving force of relationships between demographic parameters. It would be useful to test whether costs of reproduction are evident in the captive timber elephant population, or whether individual quality is the dominant process, as this would be relevant to the likely impact of attempts to improve particular demographic parameters.

6.2. Long-term strategies for reproductive success in timber elephants

Over twenty months of gestation followed by three to four years of lactation is energetically extremely expensive for logging female elephants under work-related stress. An adequate availability of nutrients during gestation is probably the most important environmental factor influencing the probability of conception and the outcome of pregnancy. An inadequate food supply will cause a state of competition between the mother and the foetus in which the well-being of both is at serious risk (King, 2003). When logging females are pregnant they should be well-fed and retired from logging operation until the calf reaches weaning age. All possible measures should be taken to extend their reproductive life-span by improving their nutrition, especially in females in the reproductively prime age range of 25-40.

Recently studies have shown that the growth, survival and fecundity of individuals can be affected by resource availabilities under the influence of environmental conditions (Albon *et al.*, 1992; Albon *et al.*, 1986; Mysterud *et al.*, 2007; Mysterud & Ostbye, 2006). With increasing fragmentation of natural areas and a dramatic reduction of forest cover in several parts of Myanmar as the result of the ever-increasing rate of logging (Leimgruber *et al.*, 2003;

Leimgruber *et al.*, 2005), it is critical to quantifying the survival and fecundity patterns of elephant populations working in fragmented over-logged forests and those working in intact forests with diverse food sources.

Like other mega-herbivores, foraging strategy and quality of diet determine the life-history traits of elephants. All elephants in the same habitat may not have the same diet. Although I was unable to quantify the foraging strategy in the timber elephants of Myanmar, I assumed that Asian male elephants need longer foraging time, as seen in African study (Shannon *et al.*, 2006), due to their preference on low quality diet. High mortality of bulls in my study also signifies insufficient nutrition to meet their body requirement resulting from inadequate foraging and strenuous logging work. More research is needed to determine the foraging strategy of captive-born and wild- caught elephants and the differences between sexes and different age-groups.

Further work is required on the relationship of musth frequency and male survival probability. It would also be worthwhile to determine the impact of nutrition and work load on musth frequency by comparing the musth records of elephants working in heavily-logged over-exploited forest and those in forests with limited logging and better vegetation.

Faster growth in males has acted on mothers to invest more resources in male offspring compared to female offspring (Maynard Smith, 1980; Trivers & Willard, 1973). Elephant mothers with suckling sons should be given special attention to be well-provisioned in order to maintain their lactating ability and prolong the bonding of mother and her calf. Mother-calf attachment is crucial during the pre-weaning stage, in order to reduce the vulnerability of calves from predation and accidents. In ungulates, the spatial relationship between the adult female and its neonate is affected by the calf's gender, as male calves exhibited higher levels of locomotor activity than female calves (more walking and playing)(Mathisen et al., 2003). Calves' maternal independence due to high levels of locomotive activities are likely to suffer high predation rates or to face accidents. Similar findings have been documented in reindeer calves (Mathisen *et al.*, 2003), bison (Green, 1992), African elephants (Lee & Moss, 1986) and free-ranging beef cattle (Lidfors & Jensen, 1988).

Elephant maternal rearing strategies are the result of a complex interaction between maternal age, maternal body size or condition, the sex of calf (which determines its need for energy intake to sustain growth) and her past experience or learning opportunities from older herd mates (Lee& Moss, in press). Allocate mothers are of great assistance in helping raise calves. One of the major gaps in this thesis is that the data are not available to address the contributions of allocate mothers, older herd-mates and grandmothers in calf-rearing.

However, I would like to look to the future, and discuss how we can move forward in our understanding of the observed phenomena. To prevent calf mortality or to boost breeding rate, calves born in captivity should be weaned gradually with the help of supplements to avoid wasting mothers' resources through suckling. A relatively long period when milk is supplemented by solid food is advantageous for the mother. She does not then have to supply the total calorific needs of the young during lactation and she can benefit by regaining reproductive cyclicity through the shortening of the lactational amenorhea. On the other hand, an extended absolute length of the mixed-feeding period is advantageous for the offspring because energy is supplied by the solid food and supplemented by milk.

Animals that eat high-quality food are characterized by faster growth rate and a relatively short weaning period (Langer, 2003) and have a higher chance of surviving. Studies have shown that offspring of large-bodied mammals, such as the anthropoid primates, ungulates and pinnipeds can safely be weaned when a neonate has grown to four times its birth weight, depending on maternal abilities to meet energetic requirements of the offspring through lactation after infants attain a threshold weight (Lee *et al.*, 1991). More research is needed to determine the best age or body mass for weaning in elephants. This also raises the issue of developing the most appropriated replacement milk formula or milk supplement for calves if elephant mothers are unable to produce sufficient milk. The further work recommended here would be of benefit in improving the effective, humane management of the captive timber elephant population in Myanmar, as well as in helping to conserve wild elephant populations by minimising direct impacts on them. It is also suggested that the Myanmar Government should attempt to remodel the traditional dragging gear through inputs of modern technology and management, aiming to increase the elephants' hauling capacity, which would result in huge economic benefits and concurrently reduce animal suffering.

Age has been used throughout this thesis, as a categorial variable in exploring survival and fecundity of captive elephants, and in comparisons between birth-origins. In mammalian demography, body size/mass has been regarded as an alternative to age as an important demographic variable (Bowen *et al.*, 2006; Sauer & Slade, 1987) in predicting fecundity and survival of a female and her offspring (Barrett *et al.*, 2006). The other questions which have not been adequately addressed in this thesis, include maternal expenditure during lactation through changes in adult body mass by parity or by sex of calf, and the relationship of maternal body mass to the survival and growth rate of offspring, in terms of birth mass, weaning mass, weaning success and lactation length in calves born to captive-born and wild-caught females. I have also shown that survival of captured elephants differs by capture method, with elephants captured by immobilization showing the lowest survival rate when compared with elephants captured by milarshikar and stockade. Clearly, more robust analyses are required to quantify differences in reproductive strategies of wild-caught elephants by capture method. I sincerely hope that this thesis will give the basic platform for conservationists and biologists to explore the remaining gaps in the future.

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Appendix I. Life table for the female wild-caught sector of captive timber elephant population

Age	Deaths	Loss/escape stolen censored	Captures	f_x	q_xWC	l_x	m_x	l_xm_x	xl_xm_x
0	0	0	5	0		1.000			
1	0	0	8	5		1.000			
2	2	2	18	13	0.154	1.000			
3	3	3	52	29	0.103	0.846			
4	6	6	86	78	0.077	0.759			
5	5	5	121	158	0.032	0.700			
6	13	17	86	274	0.047	0.678	0.003	0.002	0.014
7	11	20	56	343	0.032	0.646	0.006	0.004	0.026
8	5	11	50	379	0.013	0.625	0.003	0.002	0.013
9	9	14	73	418	0.022	0.617	0.000	0.000	0.000
10	13	24	35	477	0.027	0.604	0.004	0.003	0.026
11	5	16	40	488	0.010	0.587	0.000	0.000	0.000
12	6	13	22	512	0.012	0.581	0.000	0.000	0.000
13	7	20	53	521	0.013	0.574	0.018	0.010	0.132
14	8	9	40	554	0.014	0.567	0.009	0.005	0.074
15	8	20	30	585	0.014	0.559	0.011	0.006	0.090
16	10	17	28	595	0.017	0.551	0.014	0.008	0.124
17	7	18	38	606	0.012	0.542	0.009	0.005	0.079
18	9	26	18	626	0.014	0.535	0.027	0.015	0.263
19	11	18	55	618	0.018	0.528	0.018	0.010	0.184
20	9	24	4	655	0.014	0.518	0.031	0.016	0.326
21	12	31	27	635	0.019	0.511	0.025	0.013	0.272
22	6	21	21	631	0.010	0.501	0.027	0.014	0.299
23	10	23	21	631	0.016	0.497	0.041	0.020	0.466
24	6	17	49	629	0.010	0.489	0.030	0.015	0.351
25	14	37	17	661	0.021	0.484	0.034	0.017	0.417
26	8	27	9	641	0.012	0.474	0.036	0.017	0.437
27	5	16	25	623	0.008	0.468	0.017	0.008	0.216
28	15	31	7	632	0.024	0.464	0.035	0.016	0.451
29	9	19	56	608	0.015	0.453	0.036	0.016	0.474
30	17	43	17	645	0.026	0.447	0.036	0.016	0.479
31	14	48	13	619	0.023	0.435	0.027	0.012	0.362
32	13	44	9	584	0.022	0.425	0.038	0.016	0.518
33	13	39	8	549	0.024	0.415	0.036	0.015	0.499
34	12	26	52	518	0.023	0.406	0.030	0.012	0.419
35	20	45	7	544	0.037	0.396	0.033	0.013	0.456
36	16	37	9	506	0.032	0.382	0.033	0.013	0.453
37	17	42	9	478	0.036	0.370	0.021	0.008	0.289

38	11	34	5	445	0.025	0.356	0.025	0.009	0.341
39	12	33	17	416	0.029	0.348	0.045	0.016	0.611
40	12	31	9	400	0.030	0.338	0.036	0.012	0.488
41	21	41	4	378	0.056	0.327	0.027	0.009	0.367
42	8	31	5	341	0.023	0.309	0.030	0.009	0.392
43	6	29	3	315	0.019	0.302	0.029	0.009	0.377
44	11	30	14	289	0.038	0.296	0.031	0.009	0.407
45	10	22	2	273	0.037	0.285	0.025	0.007	0.323
46	7	21	1	253	0.028	0.275	0.032	0.009	0.401
47	11	17	0	233	0.047	0.267	0.015	0.004	0.183
48	11	25	1	216	0.051	0.254	0.027	0.007	0.324
49	11	20	0	192	0.057	0.241	0.012	0.003	0.141
50	12	19	4	172	0.070	0.228	0.026	0.006	0.298
51	4	9	0	157	0.025	0.212	0.021	0.004	0.227
52	4	17	0	148	0.027	0.206	0.023	0.005	0.245
53	9	21	0	131	0.069	0.201	0.026	0.005	0.278
54	6	14	2	110	0.055	0.187	0.020	0.004	0.204
55	8	18	0	98	0.082	0.177	0.000	0.000	0.000
56	9	13	3	80	0.113	0.162	0.028	0.005	0.256
57	7	9	0	70	0.100	0.144	0.032	0.005	0.265
58	7	9	0	61	0.115	0.130	0.019	0.002	0.141
59	4	13	0	52	0.077	0.115	0.023	0.003	0.157
60	2	6	0	39	0.051	0.106	0.029	0.003	0.187
61	4	7	0	33	0.121	0.101	0.000	0.000	0.000
62	1	6	0	26	0.038	0.088	0.000	0.000	0.000
63	2	3	0	20	0.100	0.085	0.000	0.000	0.000
64	3	3	0	17	0.176	0.076	0.000	0.000	0.000
65	1	2	0	14	0.071	0.063	0.000	0.000	0.000
66	1	2	0	12	0.083	0.058	0.000	0.000	0.000
67	2	2	0	10	0.200	0.054	0.000	0.000	0.000
68	1	1	0	8	0.125	0.043	0.000	0.000	0.000
69	0	0	0	7	0.000	0.038	0.000	0.000	0.000
70	1	2	0	7	0.143	0.038	0.000	0.000	0.000
71	0	0	0	5	0.000	0.032	0.000	0.000	0.000
72	2	2	0	5	0.400	0.032	0.000	0.000	0.000
73	0	0	0	3	0.000	0.019	0.000	0.000	0.000
74	0	0	0	3	0.000	0.019	0.139	0.003	0.199
75	0	0	0	3	0.000	0.019	0.139	0.003	0.201
76	2	3	0	3	0.667	0.019	0.139	0.003	0.204
						R_0 WC			**0.477**
						T WC			**32.337**
						r_0 WC			**-0.023**
						Finite rate of increase (λ)			**0.977**
						% population change			**-2.262**

Appendix II. Life table for the female captive-born sector of captive timber elephant population

Age	Deaths	Loss escape stolen censored	f_x	q_x	l_x	m_x	l_xm_x	$x\ l_xm_x$
0	128	0	1562	0.082	1.000			
1	69	157	1405	0.049	0.918			
2	31	86	1319	0.024	0.873			
3	20	46	1273	0.016	0.852			
4	59	48	1225	0.048	0.839			
5	62	77	1148	0.054	0.799			
6	26	84	1064	0.024	0.756			
7	10	54	1010	0.010	0.737	0.002	0.002	0.011
8	8	47	963	0.008	0.730	0.000	0.000	0.000
9	5	51	912	0.005	0.724	0.000	0.000	0.000
10	5	41	871	0.006	0.720	0.002	0.002	0.018
11	1	47	824	0.001	0.716	0.003	0.002	0.021
12	5	45	779	0.006	0.715	0.010	0.007	0.082
13	6	26	753	0.008	0.710	0.010	0.007	0.092
14	3	35	718	0.004	0.704	0.027	0.019	0.267
15	9	39	679	0.013	0.702	0.034	0.024	0.354
16	2	43	636	0.003	0.692	0.027	0.019	0.303
17	6	38	598	0.010	0.690	0.038	0.026	0.447
18	2	29	569	0.004	0.683	0.045	0.031	0.557
19	5	16	553	0.009	0.681	0.055	0.037	0.706
20	2	20	533	0.004	0.675	0.050	0.034	0.676
21	2	12	521	0.004	0.672	0.043	0.029	0.609
22	6	16	505	0.012	0.669	0.051	0.034	0.751
23	4	20	485	0.008	0.662	0.042	0.028	0.640
24	4	20	465	0.009	0.656	0.060	0.039	0.948
25	9	22	443	0.020	0.650	0.076	0.049	1.228
26	6	24	419	0.014	0.637	0.059	0.038	0.976
27	2	17	402	0.005	0.628	0.038	0.024	0.641
28	4	23	379	0.011	0.625	0.049	0.031	0.860
29	4	26	353	0.011	0.618	0.068	0.042	1.214
30	5	16	337	0.015	0.611	0.039	0.024	0.708
31	5	14	323	0.015	0.602	0.069	0.041	1.281
32	2	29	294	0.007	0.593	0.045	0.027	0.853
33	2	22	272	0.007	0.589	0.060	0.035	1.166
34	2	14	258	0.008	0.585	0.069	0.040	1.362
35	7	23	235	0.030	0.580	0.066	0.038	1.341
36	4	22	213	0.019	0.563	0.020	0.012	0.415

37	4	11	202	0.020	0.552	0.055	0.030	1.120
38	5	16	186	0.027	0.541	0.083	0.045	1.714
39	7	16	170	0.041	0.527	0.026	0.014	0.539
40	0	18	152	0.000	0.505	0.051	0.026	1.036
41	3	16	136	0.022	0.505	0.076	0.038	1.566
42	0	21	115	0.000	0.494	0.078	0.039	1.627
43	2	14	101	0.020	0.494	0.034	0.017	0.720
44	6	14	87	0.069	0.484	0.040	0.019	0.858
45	1	17	70	0.014	0.451	0.017	0.008	0.341
46	4	16	54	0.074	0.444	0.044	0.020	0.898
47	0	13	41	0.000	0.411	0.054	0.022	1.045
48	1	5	36	0.028	0.411			
49	1	10	26	0.038	0.400			
50	0	6	20		0.385			
						R_0 CB		**1.017**
						T CB		**29.494**
						r_0 CB		**0.001**
						Finite rate of increase (λ)		**1.001**
						% population change CB		**0.056**